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DOI: https://doi.org/10.3417/2017055

A TAXONOMIC REVISION OF *PASSIFLORA* SECT. *XEROGONA* (PASSIFLORACEAE) USING PRINCIPAL COMPONENT ANALYSIS[1]

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Abstract

In subgenus *Decaloba* (DC.) Rchb. of *Passiflora* L., the section *Xerogona* (Raf.) Killip (Passifloraceae) is a group of herbaceous vines found in subtropical and tropical regions of the Americas. Primarily distributed in Central America, with a few also found in the West Indies and South America, the species of *Passiflora* sect. *Xerogona* are recognized by their unusual dehiscent capsular fruit, the absence of bracts and laminar nectaries, and their transversely grooved seeds. *Passiflora tenella* Killip is the only species included in *Passiflora* sect. *Xerogona* with a fruit that does not appear to be a capsule, but the shape of the leaves and the absence of floral bracts and laminar nectaries suggest affiliation with this section. Fifteen species, including two subspecies, are recognized within *Passiflora* sect. *Xerogona*. *Passiflora cobanensis* Killip is distinguished as two subspecies, *P. cobanensis* subsp. *cobanensis* and *P. cobanensis* subsp. *brevipes* (Killip) T. Boza, with the latter subspecies transferred from *P. brevipes* Killip. From previous species circumscriptions, this section contains two problematic species complexes for *P. capsularis* L. and *P. rubra* L. The morphological variation between and within these two species complexes was examined in this study, using Principal Component Analysis and correlation matrices of morphological characters, and this variation was studied throughout their distributional ranges. *Passiflora capsularis* is recognized as a single variable species. Two species are recognized within the *P. rubra* complex, based primarily on floral characters, as *P. cisnana* Harms and *P. rubra*. *Passiflora cisnana* is lectotypified.

Resumen

En el subgénero *Decaloba* (DC.) Rchb. de *Passiflora* L., la sección *Xerogona* (Raf). Killip (Passifloraceae) es un grupo de lianas herbáceas encontradas en regiones subtropicales y tropicales de las Américas. Principalmente distribuido en Centroamérica, también se puede encontrar algunas en las Antillas y Sudamérica, las especies de *Passiflora* secc. *Xerogona* son reconocidas por su inusual fruto capsular dehiscente, la ausencia de brácteas y nectarios laminares y sus semillas transversalmente acanaladas. *Passiflora tenella* Killip es la única especie incluida en *Passiflora* secc. *Xerogona* con una fruta que no parece ser una cápsula, pero la forma de las hojas y la ausencia de brácteas florales y nectarios laminares sugieren la afiliación con esta sección. Quince especies, incluyendo dos subespecies, se reconocen dentro de *Passiflora* secc. *Xerogona*. *Passiflora cobanensis* Killip se distingue como dos subespecies, *P. cobanensis* subsp. *cobanensis* y *P. cobanensis* subsp. *brevipes* (Killip) T. Boza, con la última subespecie transferida de *P. brevipes* Killip. De circunscripciones anteriores de especies, esta sección contiene dos complejos problemáticos de especies para *P. capsularis* L. y *P. rubra* L. La variación morfológica entre y dentro de estas dos especies complejas se examinó en este estudio, usando el Análisis de Componentes Principales y basado en la correlación de matrices de caracteres morfológicos, y esta variación se estudió a lo largo de todos sus rangos distribucionales. *Passiflora capsularis* se reconoce como una sola especie variable. Dos especies se reconocen dentro del complejo *P. rubra*, basado principalmente en caracteres florales, como *P. cisnana* Harms y *P. rubra*. *Passiflora cisnana* es lectotipificada.

Key words: *Passiflora*, Passifloraceae, Principal Component Analysis, section *Xerogona*.

Passiflora L. (Passifloraceae) is a large genus of more than 600 species of vines and lianas primarily distributed in the New World, in tropical, subtropical, and occasionally temperate areas, but there are also about 26 species in India, Southeast Asia, Oceania, and Australia. The genus is most diverse in tropical regions of the Americas, where it is found in a variety of habitats, from deserts and floodplains to Andean slopes up to the

[1] This work was developed under the project "Untangling the passionflower vines: Phylogeny, species diversification, and character evolution in *Passiflora* subg. *Decaloba* (Passifloraceae)" and supported by the National Science Foundation (DEB-0717115 and DEB-0716940). The authors are grateful to the directors of the following herbaria for providing loans of their collections that were necessary to accomplish this study: A, AAU, AMAZ, ARIZ, AS, B, BAB, BH, BM, BR, BRH, C, CAS, CHAPA, CR, CTES, CU, CUZ, DLY, DUKE, E, EAP, ENCB, F, FCQ, G, GB, GH, HBG, HSB, HULE, HUT, IAC, K, L, LAGU, LIL, LL, LPB, M, MA, MEXU, MICH, MIN, MO, NA, NY, P, PH, PMA, PY, QCA, QCNE, RPSC, RSA, S, SCZ, SEL, SI, SLPM, SPF, TEFH, TEX, TTC, U, UC, UPS, US, USJ, USM, USZ, W, WIS, and XAL. We also give our sincere thanks to Peter Stevens for his critical comments on an earlier draft of this manuscript, and to the reviewers Christian Feuillet, Kristen Porter-Utley, and Armando Estrada for suggestions that improved the article. We would also like to thank Sara Edwards and Rodrigo Camara at Royal Botanic Gardens, Kew.

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Version of record first published online on 20 July 2018 ahead of Summer 2018 issue.
doi: 10.3417/2017055 Ann. Missouri Bot. Gard. 103: 258–313.

lower limits of the puna and páramo, and in forest margins up to 4200 m in the high Andes.

Passiflora displays a wide range of leaf shapes and much variation in the extrafloral nectaries present on leaves, bracts, and petioles. *Passiflora* has a complex floral structure and is characterized by several unique features. Its most distinctive characteristic is the corona of showy filaments, which plays a very important role in the pollination of most of the species. The innermost series of the corona, the operculum, is often basally connate and frequently membranous. The limen is a disk-shaped organ at the base of the androgynophore, which comes into contact with the operculum and together they regulate access to the annular nectary on the floor of the floral tube. The androgynophore is elongate, and the ovary is located where the stamens diverge from the androgynophore. Variation in these floral and vegetative features forms the basis of a complex taxonomic division of *Passiflora* into subgenera, supersections, sections, and series (Harms, 1925; Killip, 1938; Muschner et al., 2003; Feuillet & MacDougal, 2003).

Passiflora comprises six subgenera: *Passiflora* subg. *Astrophea* (DC.) Mast. (ca. 60 species), *Passiflora* subg. *Decaloba* (DC.) Rchb. (ca. 250 species), *Passiflora* subg. *Deidamioides* (Harms) Killip (six species), *Passiflora* subg. *Passiflora* (ca. 275 species), *Passiflora* subg. *Tetrapathea* (DC.) P. S. Green (three species), and *Passiflora* subg. *Tryphostemmatoides* (Harms) Killip (seven species). Species numbers are according to Feuillet and MacDougal (2003), Krosnick et al. (2013), and unpublished updates including incremental additions of recently published species. *Passiflora* subg. *Decaloba* includes herbaceous climbers and lianas with significant morphological variation and ecological diversity. The most remarkable variation can be seen in leaf shape, with the blades resembling swallowtail butterflies, shields, sausages, duck feet, boomerangs, kitten heads, coins, and half moons; there is also variation in blade variegation, as well as the arrangement of extrafloral nectaries on the petioles or laminas. Flowers range from green, small, and less than 1 cm in diameter, to white and ca. 3 cm in diameter, or red with a long androgynophore to 12 cm long.

Feuillet and MacDougal (2003) divided *Passiflora* subg. *Decaloba* into eight supersections: *Passiflora* supersect. *Auriculata* J. M. MacDougal & Feuillet (eight species), *Passiflora* supersect. *Bryonioides* (Harms) J. M. MacDougal & Feuillet (22 species), *Passiflora* supersect. *Cieca* (Medik.) J. M. MacDougal & Feuillet (19 species), *Passiflora* supersect. *Decaloba* (DC.) J. M. MacDougal & Feuillet (121 species), *Passiflora* supersect. *Disemma* (Labill.) J. M. MacDougal & Feuillet (21 species), *Passiflora* supersect. *Hahniopathanthus* (Harms) J. M. MacDougal & Feuillet (five species), *Passiflora* supersect. *Multiflora* (Small) J. M. MacDougal & Feuillet (22 species), and *Passiflora* supersect. *Pterosperma* (L. E. Gilbert & J. M. MacDougal) J. M. MacDougal & Feuillet (four species). Seven of these supersections occur in the New World and one supersection, *Passiflora* supersect. *Disemma*, is found in the Old World. In *Passiflora* supersect. *Decaloba*, the leaves are mostly 2-lobed by the reduction of the central lobe of a 3-lobed lamina. The laminar nectaries often appear as ocellae between the principal blade veins, but there are no petiolar nectary glands. Two sections have been recognized within *Passiflora* supersect. *Decaloba*: section *Decaloba* DC., consisting of approximately 106 species, and section *Xerogona* (Raf.) Killip, which includes the 15 species considered herein. These 15 species are characterized by their unusual dehiscent capsular fruit, with only one exception, *P. tenella* Killip, which has an indehiscent berry. The fruits of all other passifloras are berries, although a few of these species have irregular dehiscence, as seen in *Passiflora* supersect. *Bryonioides* (MacDougal, 1994). Killip (1938) placed *Xerogona* as a section within *Passiflora* subg. *Plectostemma* Mast., now *Passiflora* subg. *Decaloba* (Feuillet & MacDougal, 2003), based primarily on seed and fruit morphology, and the lack of bracts. The present taxonomic revision focuses on species of *Passiflora* supersect. *Decaloba* sect. *Xerogona* s. str.

Within *Passiflora* sect. *Xerogona* the Central American species are well defined, while two species complexes in South America and in the Caribbean Islands are difficult to separate; they are traditionally identified as the *P. capsularis* L. species group and the *P. rubra* L. group. Each complex displays overlapping morphological variation between the groups, and they are often difficult to distinguish. The three most useful features to differentiate between the two complexes are the indumentum of the ovary, the shape of the fruit (Killip, 1938; Holm-Nielsen et al., 1988; Amorim et al., 2014), and the color of the corona (Killip, 1938; Ulmer & MacDougal, 2004). A recently found distinction is of the satellite chromosome pairs that show different centromeric positions, submetacentric in *P. capsularis* and metacentric in *P. cisnana* Harms (as "*P. rubra*," Amorim et al., 2014).

Despite the extraordinary morphological diversity among and within *Passiflora* species, there are few studies that have used statistical tools to compare interspecific variation (Villacís et al., 1998; Porter-Utley, 2003, 2014; Krosnick, 2006; Ocampo Pérez, 2007; Ocampo Pérez & Coppens d'Eeckenbrugge, 2017).

Materials and Methods

Morphological data set

This study is based on the examination of the external morphology of over 1400 dried collections from more than 70 herbaria. This was supplemented with

Table 1. Quantitative and qualitative morphological characters recorded for selected herbarium specimens representing *Passiflora* L. sect. *Xerogona* (Raf.) Killip.

Organ	Quantitative characters	Code in PCA	Organ	Quantitative characters	Code in PCA
Leaf	Stipule length*	StL	Flower	Style length*	StyL
	Stipule width*	StW		Style width	
	Petiole length*	PeL		Stigma width	
	Blade lateral lobe length*	BLLbL	Fruit	Fruit length*	FL
	Blade lateral lobe width*	BLLbW		Fruit width*	FW
	Blade central lobe length		Seed	Seed length*	SeL
	Blade central lobe width			Seed width*	SeW
	Blade central vein length*	BCVL		Seed groove number	
	Blade lateral vein length*	BLVL			
	Blade lateral vein angle*	BLVA		Qualitative characters	
	Blade length in outline*	BLO	Stem	Stem shape	
	Blade width*	BW	Leaf	Stipule shape	
	Blade basal lobe length*	BBLbL		Stipule apex	
	Blade trichome length abaxial			Stipule abaxial indumentum	
Flower	Blade trichome length adaxial			Stipule adaxial indumentum	
	Number of blade lobes			Blade shape outline	
	Peduncle length with stipe			Blade base	
	Inflorescence flower number			Blade abaxial indumentum	
	Floral tube diameter			Blade adaxial indumentum	
	Floral tube length			Blade indumentum type abaxial	
	Flower diameter			Blade indumentum type adaxial	
	Sepal length*	SL		Blade surface	
	Sepal width*	SW		Petiole indumentum	
	Petal length*	PL	Flower	Sepal shape	
	Petal width*	PW		Sepal apex	
	Corona filament outer row length*	CORL		Petal shape	
	Corona filament outer row width			Petal apex	
	Corona filament inner row length			Corona filament color	
	Corona filament inner row width			Ovary shape	
	Corona filament row number			Ovary indumentum*	OvI
	Corona filament number			Ovary indumentum type	
	Androgynophore length*	AGL	Fruit	Fruit shape	
	Operculum height*	OH	Seed	Seed shape	
	Anther length*	AL			
	Anther width*	AW			

*Characters used in PCA.

observations from plants preserved in formalin-acetic acid-alcohol (FAA), photographs, and observation of living plants in the field. Herbarium specimens representing *Passiflora* sect. *Xerogona* and spanning the morphological variation and geographical range of each species were chosen for measurement. Characters were measured from corresponding positions on mature, fertile plants in order to minimize variation in developmental bias. A total of 66 morphological characters were measured or observed on the selected plant specimens. All measurements were taken from dried herbarium material, using a caliper and dissecting microscope. Because the species of *Passiflora* exhibit much morphological variation even within a single plant, the maximum and minimum measurements were recorded for each character on each specimen.

Characters chosen for measurements were based in part on those that have been previously used to differentiate species within *Passiflora* and within section *Xerogona* (see Table 1). All quantitative measurements were made in millimeters. Foliar and floral characters measured are shown in Figures 1–3. Floral characters were observed on herbarium specimens rehydrated by placing flowers in warm water. The flowers of species of *Passiflora* sect. *Xerogona* range from ca. 1.5 cm in diameter in *P. tenella* and *P. pusilla* J. M. MacDougal to more than 4 cm in diameter in several species, including *P. costaricensis* Killip, *P. rovirosae* Killip, *P. citrina* J. M. MacDougal, and *P. sanguinolenta* Mast. & Linden. Seeds were also measured in millimeters, but some photographs were taken with rulers in inches next to the seeds, which may be seen in some of the

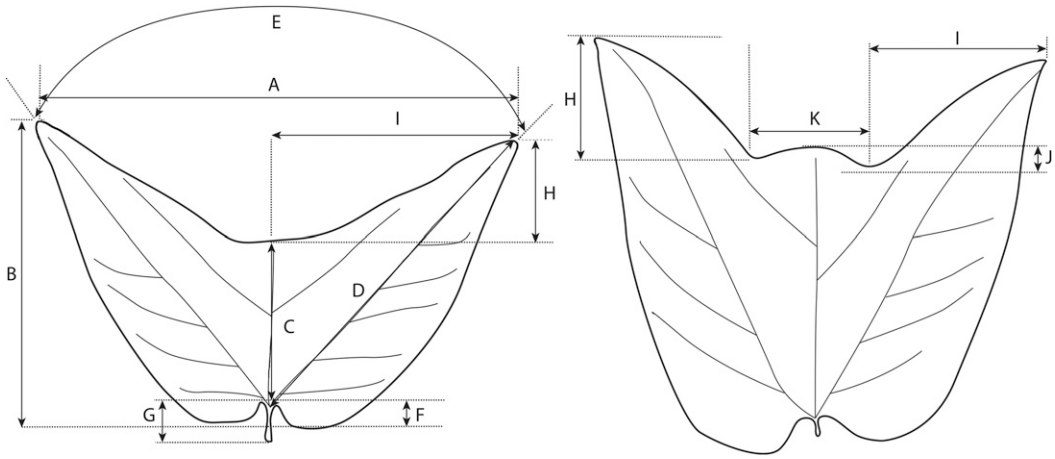

Figure 1. Diagram of leaves of *Passiflora rubra* L. illustrating measurement specifications. —A. Width of blade. —B. Length of blade. —C. Length of central vein. —D. Length of lateral vein. —E. Angle between primary lateral veins. —F. Distance from point of petiolar insertion to the base of the basal lobe. —G. Length of petiole. —H. Length of lateral lobe. —I. Width of lateral lobe. —J. Length of central lobe. —K. Width of central lobe.

photographic figures; to avoid confusion, metric scale bars were added to the photographs.

Color names follow the standardized English terminology for hues established by the Inter-Society Color Council and U.S. National Bureau of Standards (ISCC-NBS, 1965), except that pale hues around white are called whitish, and sometimes colors from labels are quoted.

Distribution maps were produced in ArcView GIS Version 9.5. The latitudes and longitudes concerning 15 species were gathered from Tropicos® and georeferenced when coordinates were not directly available in order to construct the distributional maps.

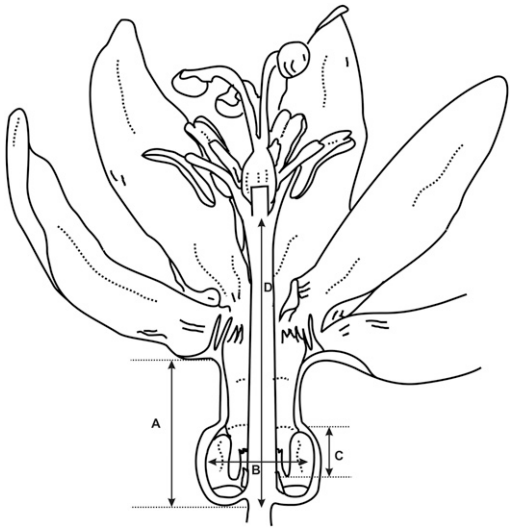

Figure 2. View of *Passiflora manicata* (Juss.) Pers. illustrating measurement specifications for the floral tube found in some species of section *Xerogona* (Raf.) Killip (modified from Jørgensen et al., 1984). —A. Length of floral tube. —B. Width of floral tube. —C. Operculum height. —D. Androgynophore length.

PRINCIPAL COMPONENT ANALYSIS (PCA)

Species of section *Xerogona* from Central America are well defined and easy to distinguish and were therefore not included in the PCA. However, in the traditional sense (Killip, 1938; Holm-Nielsen et al., 1988), *Passiflora capsularis*, *P. rubra*, and later *P. cervii* M. A. M. Azevedo (Milward-de-Azevedo, 2008) have been difficult to distinguish and are morphologically very variable. Since pre-Linnaean times doubts have existed about how and if these species are differentiated (Linnaeus, 1753), and 17 names have been published that are currently considered synonyms within the complexes. In order to find distinguishing characters and reach a better understanding of their morphological variation, PCA was carried out on the *P. capsularis* and *P. rubra* complexes, which included the closely related *P. cervii*.

Principal Components Analysis (PCA) is a useful statistical method to evaluate morphological variation. It has been used to circumscribe taxa of plants from the Bromeliaceae (Gardner, 1983), Passifloraceae (Porter-Utley, 2003, 2014; Ocampo Pérez, 2007; Ocampo Pérez & Coppens d'Eeckenbrugge, 2017), Fabaceae (Castro et al., 2005), Arecaceae (Henderson, 2004, 2006), and the Calceolariaceae (Puppo, 2008), among others. The data used in the PCA were the mean values of measurements taken from each specimen. Only 25 quantitative and one qualitative characters were used in the analyses (Table 1). A total of 130 collections provided data for the analyses of *Passiflora capsularis*, *P. cervii*, and *P. rubra* (Appendix 1). The rare and recently described *P. cervii* is represented in this analysis by

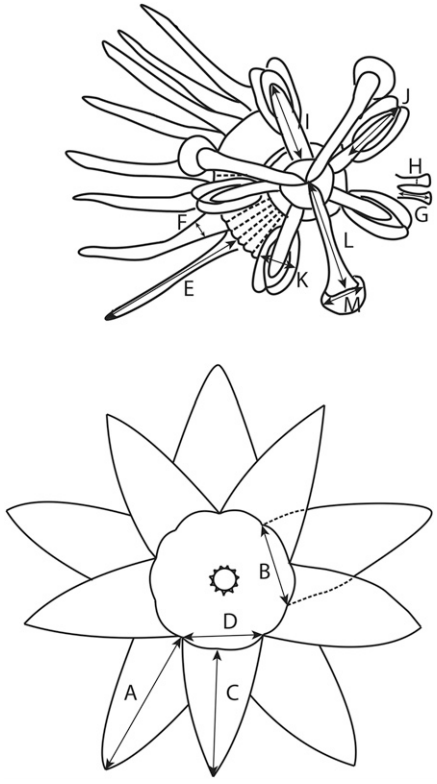

Figure 3. Frontal views of subgenus *Decaloba* (DC.) Rchb. flower illustrating measurement specifications (modified from Porter-Utley, 2014). —A. Length of sepal. —B. Width of sepal. —C. Length of petal. —D. Width of petal. —E. Length of outer corona filament. —F. Width of outer corona filament at midpoint. —G. Length of inner corona filament. —H. Width of inner corona filament. —I. Length of staminal filament. —J. Length of anther. —K. Width of anther. —L. Length of style. —M. Width of stigma.

three collections. Data has been stored in the Tropicos® database, and a matrix was built using the variables listed in Table 1.

Data analyses were carried out using SPSS 17.0. The one-sample Kolmogorov-Smirnov test was performed to test the normality of the data. Outlier points were checked with box plots. Only those axes corresponding to components with eigenvalues greater than 1.0 were extracted, and the individuals were projected on the first three PCA components.

Twenty analyses were run; only the four most relevant are included here. The specimens listed in Appendix 1 were separated into two sets (Table 2). The first set included all the data of the *Passiflora capsularis* and *P. rubra* complexes and *P. cervii*. The second included the specimens of the P. rubra complex and P. cervii The second set included the specimens of the *P. rubra* complex and *P. cervii*.

Since there is little overlap between flowering and fruiting periods, only approximately 12% of the specimens (15 out of 130) could be scored for all characters that included states for the fruit and seed. Thus, PCA for foliar and floral characters, both combined and for floral characters separately, were carried out for each species complex. Results are represented as bivariate scatter plots (Fig. 4).

Results

Principal component analyses for the species complexes in *Passiflora* sect. *Xerogona*

The PCA 1i (Fig. 4A) included only floral characters. The two first components accounted for approximately 24% and 20% of the variance. Characters that loaded heavily on the first component axis were sepal width (SW) (for character codes, see Table 1), corona outer row length (CORL), and sepal length (SL). The characters providing the principal variability in the second component were petal width (PW), petal length (PL), and anther width (AW). The scatter plot for the floral variation across the section (Fig. 4A) shows two coherent but only weakly distinguished groups, *Passiflora capsularis* and *P. rubra*, with almost no overlap. *Passiflora cervii* fell within the morphological space occupied by *P. rubra*.

The PCA 1ii (Fig. 4B) included all measured specimens with all coded characters, both fertile and vegetative, and suggested that there are four distinct specimen groupings: (1) a *Passiflora capsularis* group; (2) a Caribbean group, with *P. rubra*; (3) a South American group, also including *P. rubra*; and (4) *P. cervii*, close to the South American group with *P. rubra*. Both groupings found in association with *P. rubra* are here

Table 2. The four most relevant PCA data sets for analysis of *Passiflora capsularis* L., *P. cervii* M. A. M. Azevedo, and *P. rubra* L., including the number of specimens and number of morphological characters available.

	Analyses	No. specimens	No. characters
1	i. All species, only floral characters	43	11
	ii. All species, all characters	15	26
2	i. *P. rubra* complex and *P. cervii*, only vegetative characters	38	11
	ii. *P. rubra* complex and *P. cervii*, all characters	12	26

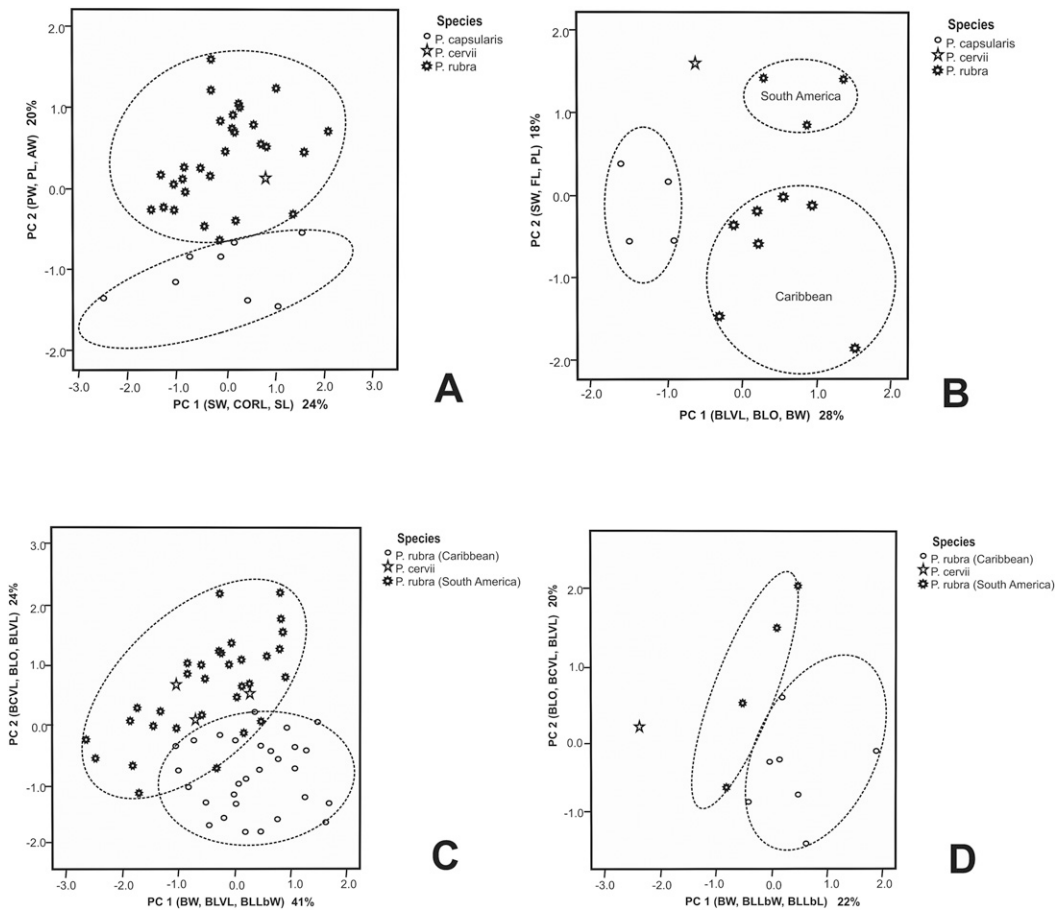

Figure 4. Bivariate scatter plots of the PCA results for *Passiflora capsularis* L. and *P. rubra* L. complexes, including the closely related *P. cervii* M. A. M. Azevedo. See Table 1 for character codes. See Table 2 for analyses performed. —A. PCA 1i. All species, floral characters only. —B. PCA 1ii. All species, all characters. —C. PCA 2i. *Passiflora rubra* and *P. cervii*, vegetative characters only. —D. PCA 2ii. *Passiflora rubra* and *P. cervii*, all characters.

recognized as separate species (see taxonomic treatment), with the name *P. rubra* applied to the Caribbean group and *P. cisnana* used for the South American specimen grouping. The first three components explained ca. 28%, 18%, and 12% of the variance, respectively. Characters that influence the variance of the first component (x-axis in Fig. 4B) included the blade lateral vein length (BLVL), blade length in outline (BLO), and blade width (BW). Sepal width (SW), fruit length (FL), and petal length (PL) explained most of the variation in the second component (y-axis in Fig. 4B), while petal length (PL), petal width (PW), and blade lateral vein angle (BLVA) loaded heavily on the third component.

To see whether vegetative characters alone can differentiate among *Passiflora capsularis*, *P. rubra*, and *P. cervii*, we analyzed a dataset with only foliar characters. In the PCA scatter plot (not shown), *P. capsularis* and *P. rubra* were not clearly separated, with the species overlapping considerably. This demonstrates the vegetative similarities between the three. The specimens of both species complexes (*P. capsularis*, *P. rubra*) have either 2- or 3-lobed leaves, and *P. cervii* has 3-lobed leaves. Leaf morphology was supported as extremely variable, even within one individual, and cannot be used by itself to distinguish the species.

The scatter plot of the variation in vegatative and floral characters (not shown) displayed two groups when both vegetative and floral characters were scored for *Passiflora rubra*, *P. cervii*, and *P. rubra*. As with the PCA of floral characters alone, there was very little overlap between the *P. capsularis* and *P. rubra* complexes, and specimens of *P. cervii* appeared within the *P. rubra* complex. A scatter plot of the variation among vegetative, fruit, and seed characters (also not shown) indicated an overlapping area between *P. capsularis* and the *P. rubra* complexes. Similar to the analysis of vegetative characters, *P. cervii* appeared in the overlapping area. From these initial analyses, we conclude

that *P. capsularis* and *P. rubra* are indeed two distinct species, that *P. rubra* may be subdivided into two species (*P. rubra* and *P. cisnana*), and *P. cervii* is likely distinct from *P. rubra*.

Analyses of the *Passiflora rubra* complex and *P. cervii* (PCA 2; Fig. 4C, D) examined the morphological distinctness of the two species and if *P. rubra* in the classical sense was composed of two species. The *P. rubra* complex encompasses a group of similar species that have been variously circumscribed by previous authors (Lamarck, 1789; Velloso, 1827 [1831]; Roemer, 1846; Harms, 1894).

In PCA 2i (Fig. 4C) we used exclusively vegetative characters and saw substantial overlap between Caribbean and South American specimens of *Passiflora rubra*, whereas *P. cervii* appeared with South American specimens of *P. rubra*. The first component in the PCA (Fig. 4C, x-axis) accounted for 41% of the variance, while the second and third components accounted for 24% and 10% of the variance, respectively. Characters that loaded on the first component included the blade width (BW), blade lateral vein length (BLVL), and blade lateral lobe width (BLLbW). The second component was explained by blade central vein length (BCVL), blade length in outline (BLO), and blade lateral vein length (BLVL).

PCA 2ii (Fig. 4D), where we used vegetative and floral characters, resulted in the recognition of two coherent but not sharply separated groups within *Passiflora rubra*, and the single specimen of *P. cervii* appeared separately from these two groups. All Caribbean specimens sorted as one group, and the second grouping consisted of only South American specimens. The first three components accounted for 22%, 20%, and 18% of the total variance, respectively. The characters that explained most of the variation for the first component (Fig. 4D, x-axis) were blade width (BW), blade lateral lobe width (BLLbW), and blade lateral lobe length (BLLbL). The second component (Fig. 4D, y-axis) was explained by leaf characters such as blade length in outline (BLO), blade central vein length (BCVL), and blade lateral vein length (BLVL). *Passiflora cervii* is separated by its broad 3-lobed leaves. South American specimens have either 2- or 3-lobed leaves while Caribbean specimens have 2-lobed leaves. These two groups are adjacent probably because they share the character of having 2-lobed leaves.

The scatter plot of the variation in floral characters (not shown) displayed no grouping within *Passiflora rubra*; however, *P. cervii* was quite separate. *Passiflora cervii* is distinguished by a puberulous ovary while South American and Caribbean specimens of *P. rubra* consistently have hirsute ovaries. The PCA of the combined vegetative and floral characters (scatter plot not shown) largely presents the same pattern as the previous analysis (Fig. 4D). Specimens were again clustered in two overlapping groups, but *P. cervii* differed in falling within the group of South American specimens.

Discussion

Principal component analyses for the *Passiflora capsularis* and *P. rubra* species complexes

The PCA of the quantitative morphological characters for the *Passiflora capsularis* and *P. rubra* complexes support the delimitations from earlier taxonomic treatment (Killip, 1938; Holm-Nielsen et al., 1988). However, it was not until an analysis of the floral characters alone was undertaken that *P. capsularis* and *P. rubra* became phenetically separable. Floral characters such as indumentum of the ovary (Killip, 1938; Holm-Nielsen et al., 1988) and the color of the corona (Killip, 1938; Ulmer & MacDougal, 2004) had been previously used as the most important features to differentiate between the two complexes; the analysis of floral characters herein provides more characters to differentiate the two. Characters such as sepal and outer corona filament morphologies, petal length and width, anther width, style length, operculum height, and ovary indumentum explained most of the variation of the components in the analyses. However, these taxa can also be distinguished mainly by the shape of the fruit (Killip, 1938; Holm-Nielsen et al., 1988), and this character was not included in the analyses. In *P. capsularis*, fruits are fusiform or broadly fusiform with a more abruptly tapering apex or may be more or less obovoid, slightly to sharply hexagonal, and glabrous; in *P. rubra*, fruits are distinctively globose to obovoid, hexagonal, and hirsute. The size of seeds and the sculptural designs of the sclerotesta have been noted to present good taxonomic characteristics in species of *Passiflora* (Killip, 1938; Tillett, 1988; MacDougal, 1994; Vanderplank, 1996; Deginani, 2001; Ulmer & MacDougal, 2004; Pérez-Cortéz, 2007; Estrada & Rodríguez, 2009), and *P. capsularis* and *P. rubra* are no exceptions. The seeds of both taxa are almost of the same size and are transversely sulcate, but differ in shape. The seeds of *P. capsularis* have a large projection or beak on the chalazal end that is inclined toward the raphe, while in *P. rubra* the projection is almost always reduced and much less evident.

In addition, *Passiflora capsularis* and *P. rubra* have slight differences in leaf shape and flower morphology. *Passiflora capsularis* has broadly obovate to depressed obovate leaves that almost always have two lobes. *Passiflora rubra* also has very broadly obovate (in South American specimens) to depressed obovate leaves (in Caribbean specimens) that have two lobes. However, these quantitative data overlap in morphological space,

Table 3. Summary of qualitative characters that usually separate species in the *Passiflora capsularis* L. and *P. rubra* L. complexes.

Character	*P. capsularis*	*P. cervii*	*P. cisnana*	*P. rubra*
Leaf shape (outline)	broadly obovate to depressed obovate	very broadly obovate	very broadly obovate, rarely depressed obovate (*Silverstone-Sopkin et al. 2573, Silverstone-Sopkin & Giraldo Gensini 6184, Ule 6546*)	broadly obovate to depressed obovate
Leaf lobe number	2- or 3-lobed	3-lobed	2- or 3-lobed	2-lobed
Leaf indumentum (abaxial)	densely hirsute	densely villous	densely hirtellous	densely hirsute
Leaf indumentum (adaxial)	sparsely hirsute	sparsely villous	densely hirsute	sparsely hirsute
Peduncles	solitary	solitary	solitary, very rarely in pairs in Ecuador (*Lewis & Klitgaard 3077, Smith 2046*)	solitary or in pairs
Sepal apex	acute, rarely acuminate (Brazil and Guatemala)	acuminate	acute, rarely acuminate or rounded (coastal Ecuador and northwestern Peru)	slightly acuminate to slightly rounded
Petal length (in relation to sepals)	about 1/2 to 3/4 as long as the sepals	about 2/3 as long as the sepals	about 1/2 as long as the sepals, or 3/4 as long (northwestern Peru, coastal Ecuador, southwestern Colombia, coastal Venezuela, and Guyana)	more than 3/4 as long as the sepals, or about 1/2 as long (Bahamas, Guadeloupe, Dominican Republic, and Puerto Rico)
Petal apex	slightly praemorse, retuse or obtuse to rounded	acute	slightly praemorse to obtuse or rounded and sometimes acute (northwestern Peru and coastal Ecuador)	acute or sometimes slightly praemorse to rounded
Corona row number	1, rarely 2 (Colombia, Brazil, Argentina, and Haiti)	1	2, except in Venezuela (*Lasser 1552*) and Guyana (*Knapp & Mallet 2838*)	1 or 2
Corona filament shape	filiform	ligulate	filiform	filiform
Corona filament length (in relation to sepals and petals)	shorter than petals or in between sepals and petals	shorter than petals	shorter than petals or in between sepals and petals	in between sepals and petals or as long as the petals
Color of the corona	pure white	unknown	red, pink or purplish at base, cream to white above	red, with pink or purplish dots along the entire length, usually darker toward base, rarely white apically
Ovary shape	narrowly obovoid to fusiform or ellipsoid	ellipsoid to obovoid	ellipsoid	obovoid to subglobose
Ovary indumentum	glabrous to minutely puberulous	hispid to minutely puberulous	densely hirsute	densely hirsute
Pollen grains	prolate-spheroid	oblate-spheroid	prolate-spheroid	prolate-spheroid

Table 3. Continued.

Character	*P. capsularis*	*P. cervii*	*P. cisnana*	*P. rubra*
Fruit shape	fusiform or broadly fusiform with a more abruptly tapering apex or sub-obovoid, slightly to sharply hexagonal	obovoid or fusiform	subglobose, ellipsoid to obovoid or abruptly acute at apex, often slightly hexagonal	globose to obovoid, hexagonal
Fruit indumentum	glabrous	glabrous to subglabrous	hirsute or rarely subglabrous (*Boza & Rodriguez 2078* and *Dodson et al. 7635*)	hirsute
Seed shape	6- or 9-sulcate, with a large projection 0.5–0.7 (–1) mm on the chalazal end inclined toward the raphe	5- or 6-sulcate, presence of projection unknown	6- or 7(or 8)-sulcate, lacks distinct projection or projection very reduced (< 0.4 mm)	6- or 7-sulcate, with a small projection 0.3–0.5 mm on the chalazal end inclined toward the raphe

and the two species are very similar morphologically. Differences in the sizes of the various parts of the plant reflect the environmental conditions where the plants of these very widespread species grow (Raunkiaer, 1934), but there have been no controlled transplantation tests. Therefore, qualitative characters may be more informative about the differentiation between species. The analyses were based on mostly quantitative data, and there are no discrete breaks among and within the two species complexes. Killip (1938) and Holm-Nielsen et al. (1988) noted that the fruit characters were useful in distinguishing *P. capsularis* from *P. rubra*. However, fruit characters are not practically useful because there are relatively few specimens with ripe fruits.

Inclusion of qualitative characters include the presence, density, and type of hairs on the abaxial or adaxial leaf blade surface, the number of lamina lobes, the number of corona rows, and the presence, density, and type of trichomes on the ovary. These characters strongly support the recognition of differences between *Passiflora capsularis* and *P. rubra*. Thus, although *P. capsularis* and *P. rubra* were incompletely separated in the majority of the PCA results, both species are taxonomically recognizable and differ in their ovary indumentum and the color of the corona filaments, and by the size of floral characters (Fig. 4B), and fruit and seed morphologies (Table 3).

Passiflora cervii was recently described from Brazil by Milward-de-Azevedo (2008). This species resembles *P. capsularis* and *P. rubra* but can be differentiated from these by leaf shape, a short filamentous corona, and according to Milward-de-Azevedo (2008), oblate to spheroid pollen grains and ligulate coronal filaments (Table 3). *Passiflora cervii* was recognized to be sympatric with *P. capsularis* and allopatric with *P. rubra* (Milward-de-Azevedo, 2008; Milward-de-Azevedo et al., 2012).

In PCA 1ii (Fig. 4B), which included both fertile and vegetative characters, *P. cervii* appeared as isolated from both species complexes (*P. capsularis* and *P. rubra*). However, in the analysis that considered only vegetative characters, specimens of *P. cervii* appeared in the morphological space where both species complexes overlap (scatter plot not shown), since these species share a similar leaf morphology. The same pattern occurred when vegetative characters, with the addition of fruit, were analyzed (scatter plot not shown). The fruit of *P. cervii* can be globose as in *P. rubra* or fusiform as in *P. capsularis*, and glabrous as in *P. capsularis*, so fruit characters did not distinguish among these species. Similarly, when only floral characters are analyzed, specimens of *P. cervii* appeared within the morphological space occupied by *P. rubra* (Fig. 4A). *Passiflora cervii* is characterized by densely villous hairs on both surfaces of the 3-lobed leaf blade, a single series of corona filaments, and an ovary with a puberulous indumentum, while *P. rubra* has very densely hirsute hairs on both surfaces of the 2- or 3-lobed leaf blade, one or two series of corona filaments, and an ovary with a densely and long-hirsute indumentum. *Passiflora cervii*, *P. capsularis*, and *P. rubra* were demonstrated as morphologically similar when only quantitative data were considered.

In PCA 2ii, where *Passiflora rubra* from South America and the Caribbean and *P. cervii* were compared with coding for both fertile and vegetative characters (Fig. 4D), two adjacent groups were distinguished within the *P. rubra* complex, and *P. cervii* was isolated from both. A group of *P. rubra* specimens from the Caribbean Islands and another group of South American specimens (Fig. 4B, D) are weakly separated in morphological space. The two groups were mainly distinguished by leaf characters such as blade width (BW), blade lateral lobe

width (BLLbW), blade lateral lobe length (BLLbL), blade length in outline (BLO), blade central vein length (BCVL), and blade lateral vein length (BLVL) (Fig. 4D). When only vegetative characters of the leaves were used, the two groups overlap somewhat in morphological space (scatter plot not shown), with *P. cervii* in the space occupied by South American *P. rubra*. This group of South American specimens typically has broadly obovate leaves with two or three lobes, with the exception of a few specimens from southwestern Colombia (*Silverstone-Sopkin 2573*, *6184*), coastal Ecuador (*Boender s.n.*), and northwestern Peru (*Ule 6546*) that have depressed obovate leaves with two lobes. Caribbean specimens of *P. rubra* have broadly obovate to depressed obovate leaves that always have two lobes; *P. cervii* would share morphological space with *P. rubra* because of the 3-lobed leaves that they have in common. When only floral characters are analyzed, there were no groupings within the *P. rubra* complex because variation in these quantitative characters is limited. When both vegetative and floral characters were included (scatter plot not shown), the pattern does not change from when only vegetative characters are used; there are still two overlapping groups.

However, the pattern of variation became clear when qualitative floral characters were taken into account. Qualitative characters that were not included in the analysis, such as sepal and petal apices, the color of the outer corona, and the corona row number (monoseriate or biseriate), are helpful to differentiate South American specimens from the Caribbean specimens (Table 3). There are differences in the qualitative variation of sepals and petals. South American specimens of the *Passiflora rubra* complex are characterized by having sepals with an acute apex, petals about half as long as the sepals, and petals with a slightly praemorse to obtuse or retuse apex, while the Caribbean group is characterized by having sepals typically with an acuminate apex, and petals only slightly shorter than sepals and with an acute apex. There are differences in the series number of corona filaments, as well as their length. The South American specimens almost always have two rows of corona filaments (except only one in *Lasser 1552*, Venezuela, and *Knapp & Mallet 2838*, Guyana), and the length of the outer row of filaments is intermediate between that of the sepals and petals. The Caribbean specimens have a corona with one or two rows of filaments, and the outer row is almost always shorter than both the sepals and petals. The corona filaments also differ in these two groups: they are purplish or red at the base, yet cream to white in color apically in South America, but purple or pink dotted along their entire length in Caribbean specimens. The ovary shape is also distinctive between these two groups, being ellipsoid in the South American group and ovoid to rounded in the Caribbean group (Table 3). *Passiflora cervii* is quite separate from both specimen groups, with the most significant qualitative character being the ovary indumentum that is merely puberulous in *P. cervii* but densely hirsute in the *P. rubra* complex (Table 3).

We conclude that *Passiflora* subg. *Decaloba* sect. *Xerogona* consists of 15 species, with two subspecies, of small- to medium-sized climbing vines. There are 11 species in Central America and six species in South America. Two taxa are found in both Central America and South America, *P. capsularis* and *P. costaricensis*. *Passiflora cisnana* is widespread in South America and *P. rubra* is widespread in the Caribbean Islands (Figs. 5–7).

Passiflora cobanensis Killip is distinguished as two subspecies: *P. cobanensis* subsp. *cobanensis*, from mesic to wet uplands in Chiapas and Guatemala, and *P. cobanensis* subsp. *brevipes* (Killip) T. Boza, from hotter lowland and seasonally drier areas. This subspecies recognition is based on differences in stem, leaf, corona filaments, and ovary characters.

The morphological pattern of variation shown by all specimens assigned to the *Passiflora capsularis* and *P. rubra* species complexes indicated that these complexes are actually made up of four separate species (Fig. 4B). The *P. capsularis* complex forms a single group, while the *P. rubra* complex can be separated into two groups (Fig. 4B, D), and *P. cervii* can also be distinguished from these complexes. The *P. rubra* complex can be distinguished mainly by qualitative features as shown in Table 3, as well as by geography; one specimen group for *P. rubra* was from the Caribbean Islands and the other is from South America. The type and original description of *P. rubra* (Linnaeus, 1753) were based on material from the Caribbean Islands (MacDougal et al., 2016) and consequently the species name of *P. rubra* L. should be applied to the Caribbean group. *Passiflora cisnana* (Harms, 1894) would be the next oldest name available to apply to the South America group.

Taxonomic Treatment

The species concept used for this study is the general lineage concept of De Queiroz (1998: 63): "species are segments of population level evolutionary lineages." The species criterion we used is that of phenetic similarity (Davis & Heywood, 1973), and those discontinuities may reflect geographical, ecological, and/or reproductive isolation.

The taxonomic revision of *Passiflora* sect. *Xerogona* is based on morphological observations, with the descriptive terms and shapes following those in Hickey and King (2000) and Stearn (2004) and colors in the descriptions referring to those of fresh material and photographs, or sometimes from collectors' notes.

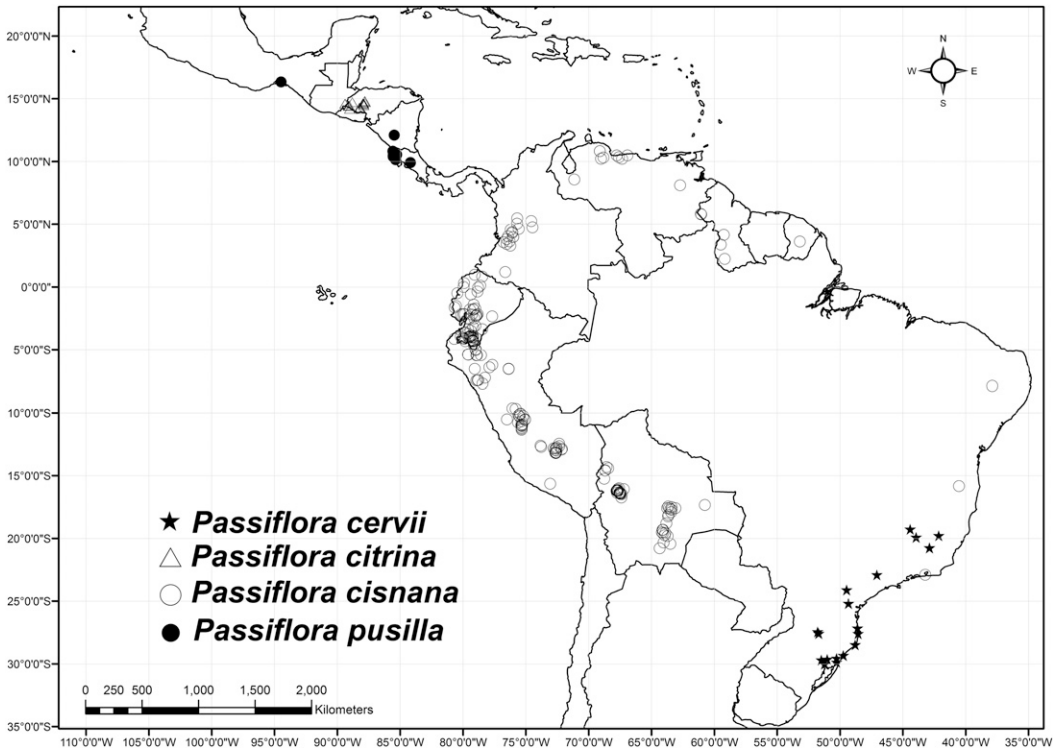

Figure 5. Distribution of *Passiflora cervii* M. A. M. Azevedo, *P. citrina* J. M. MacDougal, *P. cisnana* Harms, and *P. pusilla* J. M. MacDougal.

Every effort was made to use foliar characters in the key, since leaves are almost always diagnostic if careful measurements are taken (MacDougal, 1994), and few collectors make detailed descriptions of the flowers (Jørgensen et al., 1984).

Passiflora L. subg. **Decaloba** (DC.) Rchb. sect. **Xerogona** (Raf.) Killip, Publ. Field Mus. Nat. Hist., Bot. Ser. 19: 26. 1938. Basionym: *Xerogona* Raf., Fl. Tellur., Pt. 4: 103 1836 [1838]. TYPE: *Xerogona biloba* Raf., nom. illeg. [≡ *Passiflora capsularis* L.] (lectotype, designated by Feuillet & MacDougal [2017: 8]).

Small to medium-sized climbing perennial vines, exceptionally an annual vine in *Passiflora tenella*; stems slightly striate to 3- to 5-angular (3-keeled). Stipules linear to linear-triangular; petioles eglandular; leaf laminas with entire margins, abaxially puberulous to pubescent, adaxially puberulous to hirsute (glabrous), 2- or 3-lobed (unlobed), the lateral lobes acuminate to rounded, base cordate to rounded, laminar nectaries absent. Peduncles articulate, the distal part forming the floral stipe; bracts absent (a single linear or setaceous bract less than 4 mm at apex). Flowers with a shallow dish-shaped floral cup or floral tube; sepals narrowly oblong to triangular or narrowly triangular, not corniculate, white, pale greenish yellow, or red, often conspicuously 3-veined; petals linear to narrowly elliptic, sometimes narrowly triangular, white, pale greenish to greenish yellow, yellow, or reddish, sometimes tinged with pink or purple at the base; corona filaments in 1 or 2 series; outer filaments white, greenish with yellow apex, purple with yellow apex, or white with pink or purple at the base; inner filaments capillary or absent; operculum membranous-plicate; nectar ring present, annular; limen cupular, close to androgynophore; ovary ellipsoid, obovoid, or fusiform, minutely puberulous to densely pubescent; stigma capitate; carpels 3. Fruits fusiform, ellipsoid, subglobose, or obovoid, 6-angular to 6-keeled, reddish, purplish red, red and white, greenish, or greenish yellow, dehiscent (except terete and not dehiscent in *P. tenella*); arils white, not gelatinous; seeds transversely sulcate, the seed ridges typically smooth or less often rugulose, or with 2 longitudinal rows of teeth per face, or reduced to a row of teeth along the ridge, black or very dark brown. Germination type epigeal. Chromosome number: $n = 6$.

Discussion. Morphological/structural reduction has taken place in *Passiflora* sect. *Xerogona*, resulting in the loss of bracts and petiolar and laminar glands, which has reduced the number of characters available to distinguish the species. These lost characters have been

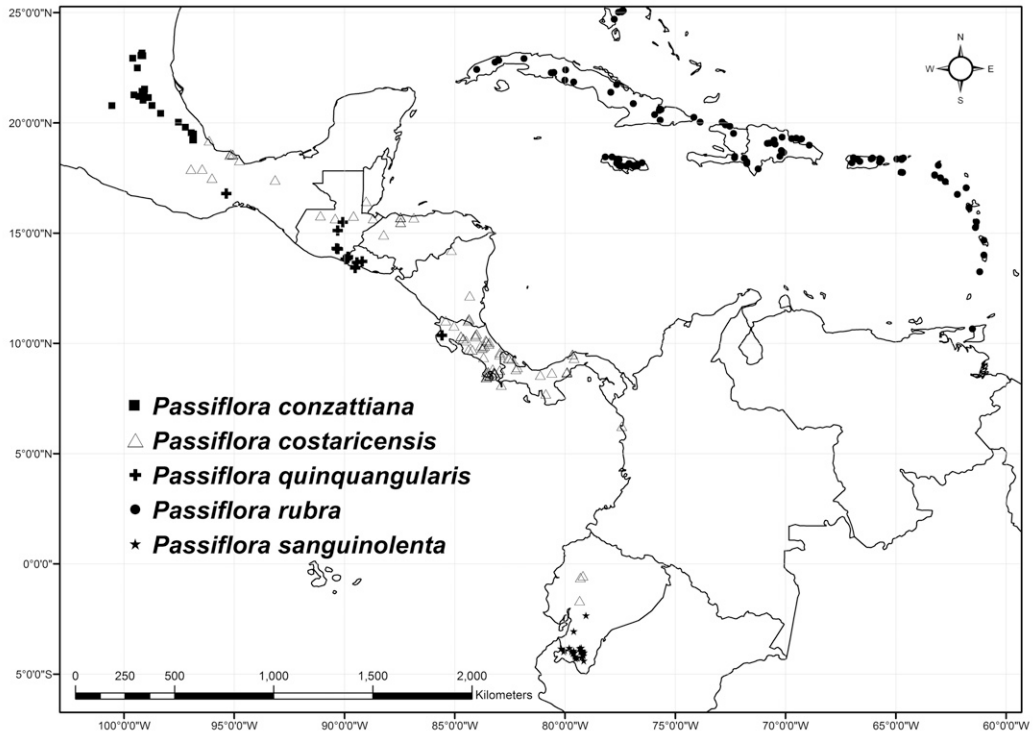

Figure 6. Distribution of *Passiflora conzattiana* Killip, *P. costaricensis* Killip, *P. quinquangularis* S. Calderón ex J. M. MacDougal, *P. rubra* L., and *P. sanguinolenta* Mast. & Linden.

frequently used elsewhere in *Passiflora* subg. *Decaloba* to discriminate among species.

Passiflora sect. *Xerogona* is characterized by its capsular fruit that dehisces in an unusual way known nowhere else among angiosperms (Peter Stevens, pers. comm.). In capsular fruits the pericarp usually dehisces along regular lines and splits to expose the seeds into as many valves as there are carpels, either septicidally or loculicidally. In *Passiflora* sect. *Xerogona*, the capsule splits into as many angles as there are in the capsule (six) and exposes the seeds along every other capsular valve, in a combination of loculicidal and septicidal dehiscence. This has also been seen in the fruit of the unrelated *P. pterocarpa* J. M. MacDougal. We were able to document this unusual fruit dehiscence in 11 species of *Passiflora* sect. *Xerogona*, with the exception of *P. cervii*, *P. conzattiana* Killip, *P. goniosperma* Killip, and *P. tenella*, from which we have insufficient material or observations. The first three exceptions mentioned have an external fruit morphology that appears to be like the other dehiscent species, with strong ridges, and we predict that these also are dehiscent at maturity. However, *P. tenella* has a fruit rather different from the other species of section *Xerogona*. Although elongated, the fruit appears to be subterete or at least not with carinae or ridges, and this may well present the outgroup condition of an indehiscent berry. In cultivated plants of *P. pusilla* J. M. MacDougal and *P. quinquangularis* S. Calderón ex J. M. MacDougal, the fruit is dehiscent to somewhat deliquescent at the apex, and it appears not to split widely.

The seeds in *Passiflora* sect. *Xerogona* are transversely sulcate, with the ridges between the grooves often smooth and shiny. However, there are some variations in the seed sclerotesta morphology. The seeds of *P. goniosperma* are strongly compressed laterally, with narrow ridges; the grooves are reduced to a row of teeth along this narrow ridge (Fig. 16E). Seeds also may have slightly rugulose ridges as in *P. sanguinolenta* (Fig. 21E) or have strongly rugulose ridges as in *P. tenella* (Fig. 22D). Other species in *Passiflora* subg. *Decaloba* typically have strongly rugulose ridges.

Epigeal germination has been observed in about half the species, corresponding to the state nearly universally known in *Passiflora* sect. *Decaloba*, and in *Passiflora* in general (MacDougal, 1994).

The chromosome counts known from 10 species in the section are uniformly $n = 6$ (Snow & MacDougal, 1993).

A variety of pollen features have also been found to be diagnostic of species within *Passiflora* sect. *Xerogona*. These features include the number and length of colpi, mesocolpia, endoaperture presence or absence, shape

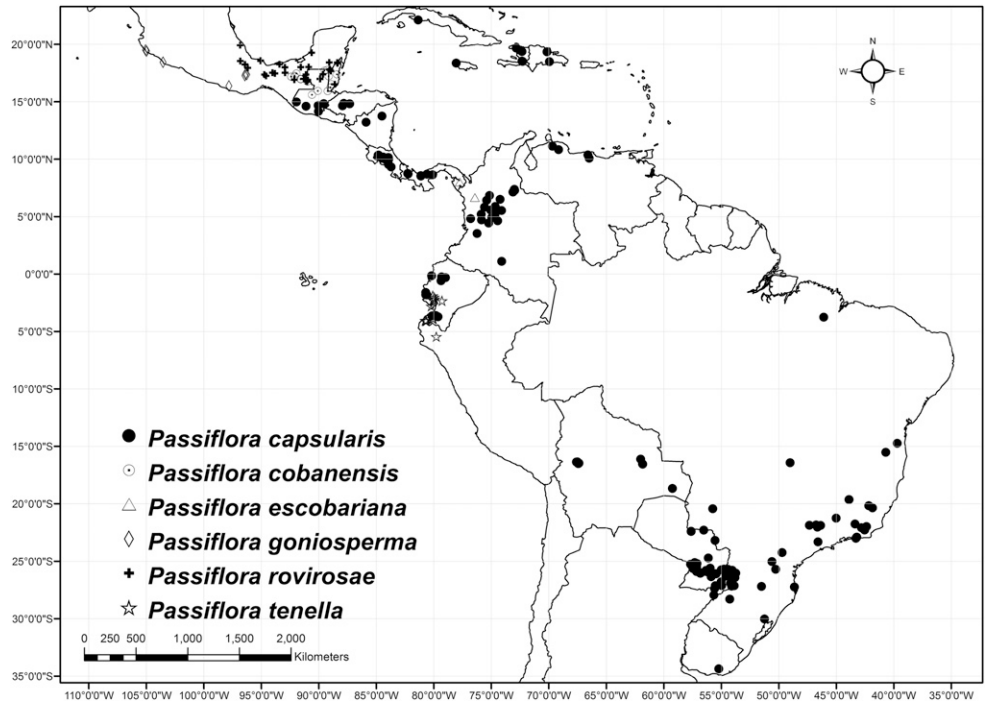

Figure 7. Distribution of *Passiflora capsularis* L., *P. cobanensis* Killip, *P. escobariana* J. M. MacDougal, *P. goniosperma* Killip, *P. rovirosae* Killip, and *P. tenella* Killip.

of muri, diameter of the reticula of the lumen, and bacula presence or absence (Presting, 1965; Huynh, 1972; Dettke, 2009; Milward-de-Azevedo et al., 2014a).

Within *Passiflora* sect. *Xerogona*, the most morphologically different species, *P. tenella*, is a small and poorly known herb from dry coastal Ecuador and Peru. *Passiflora tenella* rarely reaches 0.9 m tall and is apparently an annual plant. Its fruit is elongated but does not appear to be a capsule like other members of section *Xerogona*. The shape of the leaves and the absence of floral bracts and laminar nectaries suggest affiliation with *Passiflora* sect. *Xerogona*, and a DNA analysis places the species as sister to the rest of the section (Krosnick et al., 2013; Milward-de-Azevedo et al., 2014b).

Within *Passiflora* sect. *Xerogona*, *P. citrina* is similar to *P. sanguinolenta* in having flowers with floral tubes (vs. floral cups) that are almost the same shape and size but differ in color. The flowers of *P. citrina* are light to bright yellow while the flowers of *P. sanguinolenta* are pink to red to purplish red. The two species also differ in geographical distribution. *Passiflora citrina* is found in Guatemala, Honduras, and El Salvador, while *P. sanguinolenta* is endemic to southern Ecuador and Peru.

Passiflora cobanensis, *P. conzattiana*, and *P. goniosperma* all have small flowers with short outer corona filaments that are purplish or reddish at the base and yellow at the apex. *Passiflora cobanensis* can be differentiated from the other two by having unlobed leaves. *Passiflora conzattiana* differs from *P. goniosperma* by having seeds with transverse grooves and smooth ridges, while *P. goniosperma* has strongly compressed seeds with grooves reduced to a row of teeth.

Passiflora rovirosae is often confused by its similarity to *P. costaricensis*. However, *P. rovirosae* differs in its short indumentum and 5-angular, not 3-angular, stems. Both often bloom not far from the ground on condensed, leafless, short shoots.

Passiflora cobanensis was previously circumscribed by Killip (1938) as two different species, *P. cobanensis* and *P. brevipes* Killip, although MacDougal in 2004 recognized only a single species, *P. cobanensis*. Within *P. cobanensis*, the two variants are herein recognized as subspecies, as *P. cobanensis* subsp. *cobanensis* and *P. cobanensis* subsp. *brevipes*. The subspecies are recognized by differences in stem, leaf, corona filaments, and ovary characters. *Passiflora cobanensis* subsp. *cobanensis* is characterized by having 4- to 5-angular stems, thinner leaves that are slightly reticulate and sparsely pubescent beneath, outer corona filaments filiform with clavate apices, and ovaries glabrous or puberulous or rarely densely tomentose. *Passiflora cobanensis* subsp. *brevipes* is characterized by having only 3-angular stems, thicker leaves that are conspicuously reticulate beneath with nerves and veins elevated and densely pubescent, outer corona filaments filiform and slightly dilated toward the apices, and ovaries densely tomentose.

KEY TO THE SPECIES OF *PASSIFLORA* SECT. *XEROGONA*

1a. Leaf laminas unlobed, narrowly ovate to very broadly ovate . . . . . 5. *P. cobanensis* Killip
1b. Leaf laminas 2-lobed or 3-lobed (the central lobe, if present, reduced).
  2a. Plants smaller than 0.9 m; leaf laminas 1–5 × 2–8 cm, depressed obovate; corona filaments in 2 series.
    3a. Stems 3-angular or ± 3-angular; leaf laminas densely pubescent, lateral lobes with the apex obtuse to round; corona inner filaments white; ovary tomentose; fruit 6-keeled, dehiscent; seeds with 2 longitudinal rows of 5 or 6 teeth per face; distributed in Mexico, Nicaragua, and Costa Rica . . . . . 10. *P. pusilla* J. M. MacDougal
    3b. Stem subangular; leaf laminas sparsely pubescent, lateral lobes with the apex acute; corona inner filaments violet-tinged; ovary glabrous; fruit terete, apparently not dehiscent; seeds with 4 or 5 transverse sulci with ridges that are strongly rugulose; distributed in Ecuador and Peru . . . . . 15. *P. tenella* Killip
  2b. Plants 1–10 m or more; leaf laminas 2–16 × 2–13 cm, narrowly to broadly obovate or depressed obovate; corona filaments in 1 or 2 series.
    4a. Floral tubes present; androgynophores 15–29 mm long.
      5a. Stems 5-angular; leaf laminas broadly obovate or obtriangular; flowers light to bright yellow; corona filaments in 1, rarely 2, series; Honduras, Guatemala, and El Salvador . . . 4. *P. citrina* J. M. MacDougal
      5b. Stems 3-angular; leaf laminas depressed obovate; flowers pink to red to purplish red; corona filaments consistently in 2 series; southern Ecuador and Peru . . . . . 14. *P. sanguinolenta* Mast. & Linden
    4b. Floral tubes absent; androgynophore 2–10 mm long.
      6a. Androgynophores 2–4 mm long; outer corona filaments reddish or purplish at the base and yellowish at the apex, 2–10 mm long.
        7a. Stems 3-angular; leaf laminas 2(or 3)-lobed, depressed obovate; seeds with smooth grooves and not compressed laterally; found in east-central Mexico . . . . . 6. *P. conzattiana* Killip
        7b. Stems only slightly or shallowly 3-angular; leaf laminas 2-lobed, broadly obovate; seeds compressed laterally, with a narrow longitudinal ridge and grooves reduced to a row of teeth along ridge; found in southern Mexico . . . . . 9. *P. goniosperma* Killip
      6b. Androgynophores 4–10 mm long; outer corona filaments white, white or cream with a pink or purple base, or white with yellow tips, 5–20 mm long.
        8a. Stems 5-angular; corona filaments in 2 series.
          9a. Petioles (6–)11–14(–24) mm long; leaf laminas 2(or 3)-lobed, the angle between the lateral lobe veins (30°–)41°–50°(–68°); peduncles (18–)26–36(–90) mm long, usually solitary, rarely in pairs; floral stipe 2.2–4.8 mm long (to 5.2–8.5 mm in fruit); plants pubescent throughout; southern Mexico, Guatemala, El Salvador, and Costa Rica . . . . . 11. *P. quinquangularis* S. Calderón ex J. M. MacDougal
          9b. Petioles (12–)21–26(–35) mm long; leaf laminas 2-lobed, the angle between the lateral lobe veins (12°–)21°–26°(–35°); peduncles (5–)10–14(–25) mm long, usually in pairs; floral stipe 5.2–11.2(–25) mm long (to 5.4–18.9 mm in fruit); plants puberulous throughout; southeastern Mexico, northeastern Guatemala, and Belize . . . . . 12. *P. rovirosae* Killip
        8b. Stems 3- or 4(5)-angular; corona filaments in 1 or 2 series.
          10a. Vines 4–12 m long; leaf laminas 7–16 cm long, the angle between the lateral lobe veins 28°–59°; fruits ellipsoid or fusiform.
            11a. Stems sharply 3-angular; plants densely tomentose throughout with trichomes 0.5–2 mm long; leaf laminas 2-lobed; floral stipe 1.9–7.4 mm long (to 3.5–11.4 mm in fruit); operculi usually finely pubescent, yellowish green; androgynophores 4.4–7.6 mm long; distributed from eastern Mexico to Pacific coast of Colombia and Ecuador . . . . . 7. *P. costaricensis* Killip
            11b. Stems 4- to 5-angular; plants puberulous throughout with trichomes 0.1–0.6 mm long; leaf laminas 2(or 3)-lobed; floral stipes 2–3 mm long (to ca. 4 mm in fruit); operculi glabrous, light purple; androgynophores 7–7.6(–9.7) mm long; found in northern Colombia and eastern Panama . . . . . 8. *P. escobariana* J. M. MacDougal
          10b. Vines 2–4(–8) m long; leaf laminas 2–10 cm long, the angle between the lateral veins 32°–108°; fruits obovoid, globose, or broadly fusiform.
            12a. Ovaries glabrous to minutely puberulous.
              13a. Floral stipes 2–5 mm long (to 2–15 mm in fruit); sepals with an acute, rarely acuminate, apex; petals about 1/2 or 3/4 as long as the sepals, with a slightly praemorse, retuse, or obtuse to rounded apex; leaf laminas 2(or 3)-lobed; distributed from Central America to South America . . . . . 1. *P. capsularis* L.
              13b. Floral stipes 3.1–3.6 mm long (to ca. 8 mm in fruit); sepals with an acuminate apex; petals about 2/3 as long as the sepals, with an acute apex; leaf laminas 3-lobed; southeastern Brazil . . . . . 2. *P. cervii* M. A. M. Azevedo
            12b. Ovaries densely hirsute.
              14a. Leaf laminas 2- or 3-lobed; floral stipes 1–6.5 mm long (1.4–7.5 mm in fruit); sepals with an acute, less often acuminate or rounded, apex; petals ca. 1/2(–3/4) as long as the sepals, with a slightly praemorse to obtuse or rounded, rarely acute, apex; corona filaments in 2 (rarely 1) series, the outer filaments shorter than the petals or intermediate between sepals and petals, red, pink, or purplish at base, cream to white above; ovaries ellipsoid; South America . . . . . 3. *P. cisnana* Harms

14b. Leaf laminas 2-lobed; floral stipes 1–3.5 mm long (0.8–2.9 mm in fruit); sepals with a slightly acuminate to slightly rounded apex; petals more than 3/4 as long as the sepals (or ca. 1/2 as long) with an acute or sometimes slightly praemorse to rounded apex; corona filaments in 1 or 2 series, the outer filaments intermediate between sepals and petals or as long as the petals, with red, pink, or purplish dots along the entire length; ovaries ovoid to ± globose; Caribbean Islands . . . . . 13. *P. rubra* L.

1. Passiflora capsularis L., Sp. Pl. 2: 957. 1753. *Granadilla capsularis* (L.) Medik., Malvenfam. 96. 1787. *Xerogona biloba* Raf., Fl. Tellur. 4: 103. 1836 [1838], replacement name, nom. illeg. superfl. *Decaloba capsularis* (L.) M. Roem., Fam. Nat. Syn. Monogr. 2: 154. 1846. TYPE: tab. 1 [engraved borders on title page plate] in Barrelier, Plantae per Galliam, Hispaniam et Italiam observatae, iconibus aeneis exhibitae a R. P. Jacobo Barreliero, opus posthumum [A. de Jussieu (editor)], 1714 (lectotype, designated by MacDougal et al. [2016: 4]). EPITYPE: Haiti. Pétionville, 18°30′45″N, 072°17′07″W, 350 m, 15–28 June 1920, *E. C. Leonard 4882* (epitype, designated by MacDougal et al. [2016: 4], US-1077426 not seen, US [barcode] 00770192 image!; isoepitypes, B not seen, NY not seen). Figures 8, 23A.

Passiflora pubescens Kunth in Humb., Bonpl. & Kunth, Nov. Gen. Sp. 2: 132. 1817. *Cieca pubescens* (Kunth) M. Roem., Fam. Nat. Syn. Monogr. 2: 141. 1846. TYPE: Venezuela. Aragua, betw. Maracay & Nueva Valencia, s.d., *Humboldt & Bonpland s.n.* (holotype, P [barcode] 00252177 image!).

Passiflora capsularis var. *acutiloba* DC., Prodr. 3: 325. 1828. TYPE: Brazil. s.d., *s. coll. s.n.* (holotype, G-DC [barcode] 00201666 image!).

Passiflora bilobata Vell., Fl. Flumin. Icon 9: pl. 78. 1827 [1831], hom. illeg., non *Passiflora bilobata* Juss., Ann. Mus. Natl. Hist. Nat. 6: 107, tab. 37, fig. 2. 1805. *Passiflora piligera* Gardner, London J. Bot. 1: 173. 1842, replacement name. *Decaloba piligera* (Gardner) M. Roem., Fam. Nat. Syn. Monogr. 2: 161. 1846. *Decaloba bilobata* M. Roem., Fam. Nat. Syn. Monogr. 2: 154. 1846, nom. illeg. TYPE: tab. 78 in Vellozo, 1827 [1831].

Decaloba semilunaris M. Roem., Fam. Nat. Syn. Monogr. 2: 154. 1846. Replaced name: *Passiflora lunata* Vell., Fl. Flumin. Icon. 9: pl. 80. 1827 [1831], nom. inval.; Arch. Mus. Nac. Rio de Janeiro 5: 378. 1881, hom. illeg., non *Passiflora lunata* Sm., Arch. Bot. (Leipzig) 1: 72. 1796. TYPE: tab. 80 in Vellozo, 1827 [1831].

Passiflora paraguayensis Chodat, Bull. Herb. Boissier 7 (app. I): 74. 1899. TYPE: Paraguay. Itaguá: *E. Hassler 1419* (holotype, G not seen).

Passiflora hassleriana Chodat, Bull. Herb. Boissier 7 (app. I): 74–75. 1899. TYPE: Paraguay. Tacuaral: *E. Hassler 1202* (holotype, G not seen; isotypes, K [barcode] 000036539 image!, P [bc] 00605746!).

Passiflora hassleriana var. *grandifolia* Chodat & Hassl., Bull. Herb. Boissier ser. 2, 4: 62. 1903. TYPE: Paraguay. Bellavista, Río Apa, *E. Hassler 7913* (holotype, G not seen, G photo at MO-1680902!; isotypes, BM [barcode] 000089299 image!, GH!, K [bc] 000036540 image!, MO [bc] 2080043!, P [bc] 00605746 [2]!).

Passiflora hassleriana var. *paraguariensis* Chodat & Hassl., Bull. Herb. Boissier ser. 2, 4:62. 1903. TYPE: Paraguay. Chololo, Río Apa, *E. Hassler 6684* (holotype, G not seen).

Vines 2–4(–8) m, sparsely pubescent to glabrescent; stems 3- to 5-angular, striate, pubescent when young; later glabrescent. Stipules (1.9–)3.7–4.5(–7.4) × (0.1–)0.3–0.4(–0.7) mm, linear to linear-triangular, ± falcate, sparsely pubescent abaxially; petioles (7–)15–21(–53) mm; leaf laminas (2.4–)5–6.7(–10.8) × (2.5–)5.4–6.7(–11.8) cm, broadly obovate to depressed obovate, cordate at the base, densely hirsute abaxially with trichomes 0.1–1.1 mm, sparsely hirsute adaxially with trichomes 0.2–1.1 mm, 2(or 3)-lobed, the lateral lobes acuminate to acute, when evident, the central lobe reduced or rounded, cusplike; angle between lateral veins (37°–)56°–66°(–102°). Peduncles (12–)27–34(–62) mm, slender, solitary; floral stipe 2–5 mm, to 15 mm in fruit. Flowers (19–)31–35(–48) mm diam., white to greenish white or pale yellow-green; sepals (10.9–)14.7–16.3(–21.9) × (1.6–)2.7–3.4(–4.7) mm, narrowly triangular, sparsely hirsutulous, apex acute, but occasionally acuminate, pale green to white, rarely pink at the base; petals (4.5–)8.4–9.8(–14.6) × (1.1–)1.7–2(–2.9) mm, linear to narrowly triangular; ca. 1/2 or 3/4 as long as sepals, apex slightly praemorse, retuse or obtuse to rounded, white; corona filaments in 1(2) series; filaments of outer series 30 to 32, (6.3–)9.2–10.3(–14.4) mm, shorter than petals or between sepals and petals in length, pure white or white at base, very pale yellow distally; filaments of inner series shorter than outer series, (1.3–)2.7–2.9(–3) mm; operculum (0.6–)1.3–1.5(–2.2) mm; androgynophore 4.6–8.6 mm, green; stamens with filaments (4.3–)4.6–5.3(–5.6) mm; anthers (1.9–)3–3.2(–3.6) × (0.6–)1.1–1.3(–1.8) mm; ovary 3–5 × 2–3 mm, narrowly obovoid to fusiform or ellipsoid, glabrous to minutely puberulous, sometimes with a few scattered long trichomes distally; styles (1.6–)3.1–3.8(–5.1) × 0.2–0.3 mm; stigma (0.7–)0.9–1.2(–1.4) mm diam. Fruits (32–)45–50(–76) × (9–)14–15(–37) mm, fusiform or broadly fusiform with a more abruptly tapering apex or sub-obovoid, slightly to sharply hexagonal, glabrous, reddish brown, dark purplish red, or red, rarely white or cream between the ridges; seeds (1.3–)2.7–3(–3.9) × (1.1–)1.6–1.8(–2.1) mm, transversely sulcate with 6 to 9 sulci with a large projection 0.5–0.7(–1) mm on the chalazal end inclined toward the raphe.

Phenology. Flowers of *Passiflora capsularis* have been observed from May to December. Fruits have been

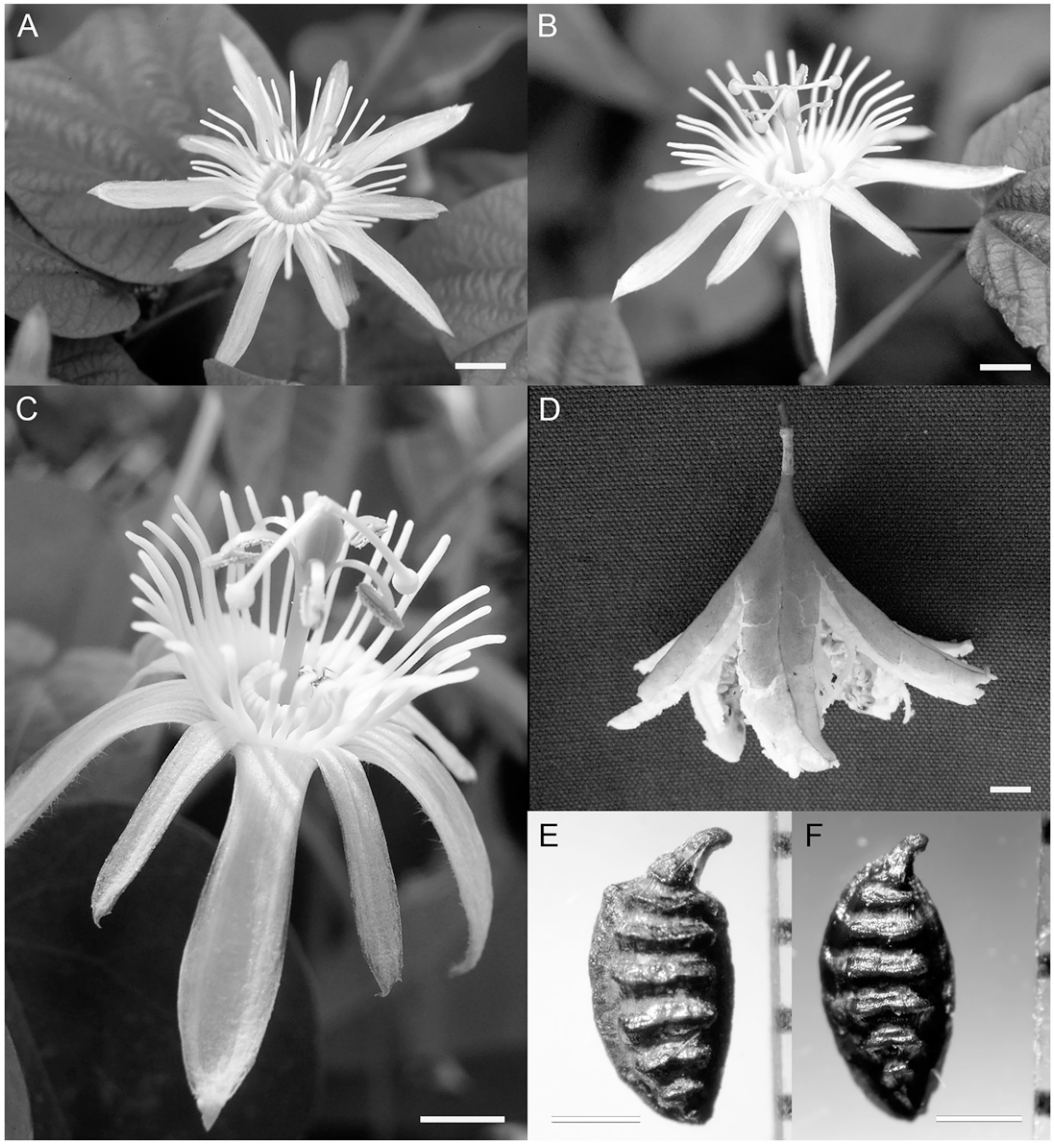

Figure 8. *Passiflora capsularis* L. —A. Flower, cultivated. —B. Flower, cultivated. —C. Flower, cultivated. —D. Dehisced fruit, Panama (*J. M. MacDougal & J. Lezcano 6269*). —E. Seed, Costa Rica (*W. C. Burger & G. Visconti 10231*). —F. Seed, Colombia (*R. Fonnegra et al. 5181*). Scale bars: A, B = 0.5 cm; C, D = 1 cm; E, F = 1 mm. Photographers: A, B, Ronald Boender; C, Jorge Ochoa; D, John MacDougal; E, F, Tatiana Boza.

documented from April to July and from December to January.

Distribution and habitat. *Passiflora capsularis* is distributed from Guatemala to Panama, Colombia, Venezuela, Ecuador, curiously interrupted and absent from Peru, and from central Brazil to Paraguay, Bolivia, and the Greater Antilles (Fig. 7). The species also has been collected from Cuba, Dominican Republic, Haiti, and Jamaica. Label records indicate the habitat to be moist, wet, rain and cloud forests from 50 to 2600 m in elevation, principally from secondary forest edges, and from secondary open areas and roadsides.

Local names. Maracuja (*P. Capell s.n.*; Brazil), mhurukuja (*Itaipú Binacional 208*; Paraguay).

Discussion. *Passiflora capsularis* and *P. rubra* have often been confused by previous authors because they are difficult to distinguish in the absence of flowers and fruits. The first description by Plumier (1693) of *P. rubra* notes that there is another very similar species in the Caribbean, and although not

naming it there, Plumier attempted to clarify the distinction between the two species, including noting that, unlike in *P. rubra*, the fruit is more elongate and pointed on both ends, and that the flower is all white, with no red.

Passiflora capsularis is characterized by having solitary flowers, sepals with apices that are acute (or rarely acuminate in Brazil), petals with slightly praemorse, retuse or obtuse to rounded apices, and petals about 1/2 to 3/4 as long as the sepals. *Passiflora rubra* has flowers solitary or in pairs, sepals with slightly acuminate to slightly rounded apices, petals with acute or sometimes slightly praemorse to rounded apices, and the petals more than 3/4 as long as the sepals (or ca. 1/2 as long). The distribution of *P. rubra* is considered more Caribbean, with specimens from Bahamas, Guadeloupe, Dominican Republic, and Puerto Rico. The corona filaments of *P. capsularis* are in one series, but rarely two series in Colombia, Brazil, Argentina, and Haiti. The outer filaments are shorter than the petals or are intermediate between sepals and petals, are white or slightly cream toward the apex, and are not marked with color (but in a dried state this difference is often not perceptible). In *P. rubra* having two series of corona filaments is more common; the outer series of filaments is intermediate between sepals and petals to as long as the petals in length, with red, pink, or purplish dots evident along the entire filament length and usually darker red toward base. The ovaries in *P. capsularis* are narrowly ovoid to fusiform or ellipsoid, glabrous to minutely puberulous or with a few scattered long trichomes; in *P. rubra*, the ovaries are obovoid to subglobose and densely pubescent with white to brown trichomes. The fruits are fusiform, or broadly fusiform with a more abrupt tapering apex or more or less obovoidal, slightly to sharply hexagonal, and glabrous in *P. capsularis*; in *P. rubra*, the fruits are globose to obovoid, hexagonal, and hirsute. The seeds of *P. capsularis* differ from those of *P. rubra* by having a longer projection 0.5–0.7(–1) mm on the chalazal end inclined toward the raphe; seeds in *P. rubra* have a shorter projection, only 0.3–0.5 mm.

Passiflora capsularis and *P. cisnana* are very similar when only vegetative characters are considered but can be distinguished when floral characters are used. *Passiflora capsularis* is characterized by having the outer corona filaments evenly whitish and unmarked by color or spots, while in *P. cisnana* the outer corona filaments can be red, pink, or purplish at the base and cream to white above. The ovary in *P. capsularis* is narrowly obovoid to fusiform or ellipsoid and glabrous to minutely puberulous or with a few scattered long trichomes, whereas in *P. cisnana* it is ellipsoid and densely hirsute. Fruit shape also differs. In *P. capsularis*, fruits are fusiform or broadly fusiform with a more abruptly tapering apex or sub-obovoid, slightly to sharply hexagonal, and glabrous; in *P. cisnana*, fruits are globose to obovoidal, hexagonal, and hirsute. The seeds of *P. capsularis* differ from those of *P. cisnana* by having a large projection 0.5–0.7(–1) mm on the chalazal end inclined toward the raphe, while *P. cisnana* seeds lack any distinct projection, or it is less than 0.4 mm.

A photo purported to be *Passiflora capsularis* from Costa Rica with a flower with a colored corona appeared in Estrada and Rodríguez (2009: 202), but it is apparently a mistake for *P. cisnana*. The photo is not of a native wild plant, but was taken in a commercial butterfly house in Costa Rica that included other exotic plants (A. Estrada, pers. comm.).

Both *Passiflora bilobata* Vell. and *P. lunata* Vell. were published only as illustrations in 1827 (Vellozo, 1827 [1831]: pl. 78, pl. 80), the first with diagnostic analysis in the plate and therefore validly published then (McNeill et al., 2012: Art. 38.7, Art. 38.8, Art. 38.9), the second without analysis and thus not valid until its description was published in 1881 (Vellozo, 1881). Both are illegitimate later homonyms of existing names in *Passiflora*, and both received replacement names by early authors. We consider these taxa to be synonyms of *P. capsularis*, agreeing with Masters (1871), Sampaio and Peckolt (1943), and Milward-de-Azevedo et al. (2012), rather than synonyms of *P. rubra* or *P. cisnana* as suggested by others (Killip, 1938; Holm-Nielsen et al., 1988; Deginani, 2001; Cervi & Rodrígues, 2010).

Passiflora piligera Gardner (1842) was published with "*Passiflora bilobata* Vellozo Fl. Flum. 9, t. 78. (non Juss.)" in synonymy and referred to Gardner's collection number *49*. Despite using the abbreviation "*sp. n.*" in his protologue, Gardner's name is clearly intended as a nomen novum for the illegitimate later homonym, and thus the type of *P. piligera* is the same as the type of *P. bilobata* Vell. (McNeill et al., 2012: Art. 7.4). Up to now, monographers have erroneously assigned type status to *Gardner 49*, with the supposed holotype at BM (Killip, 1938; Holm-Nielsen et al., 1988; Deginani, 2001; Milward-de-Azevedo et al., 2012).

Decaloba semilunaris M. Roem. (1846), based on Vellozo's pl. 80 (1827 [1831]), has as its epithet a name very similar to Vellozo's caption for pl. 80. Roemer realized that Vellozo's name was a later homonym (though not validly published by 1846 according to today's rules), so probably he intended the epithet as a kind of replacement name.

Decaloba smithii M. Roem. was considered by Killip (1938) to be a synonym of *Passiflora capsularis* L. Indeed, Roemer (1846: 161) described *D. smithii* as a replacement name for the earlier name, *P. capsularis* sensu Smith, as described by John Smith in 1819. Smith's description (1819: sp. 22) seems to fit *P. capsularis*, except

when he mentions that "there are two glands at the base of the leaf." *Passiflora capsularis* L. lacks such glands on the leaf. Smith's description and collection data match the original collection in the Smith herbarium at LINN, which is *P. tuberosa* Jacq. (LINN-HS 1418.24 image!). We have therefore eliminated *D. smithii* from the synonymy of *P. capsularis*. Two studies of floral reproductive behavior of *P. capsularis* in Brazil found that the flowers there open at night and persist into the daytime, are autogamous or self compatible, might be pollinated by both moths and bees, and lepidopteran scales were observed on some stigmas, but no legitimate pollinators were observed (Koschnitzke & Sazima, 1997; Faria & Stehmann, 2010). In contrast, greenhouse-grown clones of *P. capsularis* from Guatemala and Costa Rica were self-incompatible (MacDougal, pers. obs.).

Selected specimens examined. ARGENTINA. **Corrientes:** San Ignacio, Salto Tabay, *A. Schinini 19878* (CTES). **Misiones:** Santa Ana, 27°23′00″S, 055°35′00″W, *J. Montes 1539* (WIS); Puerto Tguozu, 5 Mar. 1945, *R. B. Hayward s.n.* (LIL); Puerto Beinbeuq, 15 Mar. 1945, *R. B. Hayward s.n.* (LIL); Victoria–Ruta 12, *E. Schwind 2421* (L, WIS); Cainguás, Mineral, *J. E. Montes 27637* (F, NY); Puerto Rico, 26°48′S, 055°01′W, *J. E. Montes 14753* (F, NY); Candelaria, Loreto, *J. E. Montes 375* (BAB); Santa Ana, 27°23′S, 055°35′W, *M. C. Romanczuk 486* (BAB, SI); General Manuel Belgrano, rt. 17 Bernardo de Irigoyen a El Dorado Km. 34, 26°22′S, 053°53′W, *F. O. Zuloaga et al. 5095* (MO, SI); Refugio de vida silv. Uruguay, FVSA, Arroyo Sauer, 25°58′S, 054°07′W, *M. E. Múlgura et al. 2712* (MO, SI); Salto Tupá, Arroyo Rodador, 26°02′S, 053°45′W, *M. E. Múlgura et al. 1909* (MO, SI); Guaraní, Sector CIFOR, 26°54′59″S, 054°12′18″W, *H. A. Keller & F. Robledo 1611* (CTES); Predio del Refugio Moconá Naturaleza y Aventura, Salto Horacio Foester, 27°08′S, 053°55′W, *M. E. Múlgura et al. 3091* (MO, SI); Rt. Prov. 2, Reserva Ecológica Prov., El Soberbio–Parque Prov. Moconá, Km. 23, 27°10′S, 054°06′W, *O. Morrone et al. 692* (MO, SI); Iguazú, Parque Nac. Iguazú, Isla San Martín, 25°41′S, 054°46′W, *F. O. Zuloaga et al. 5240* (MO, SI); Arroyo Mlocay, *T. Meyer 11814* (CTES); Cataratas del Iguazú, *T. Meyer 5912* (GH); San Pedro, Parque Prov. Cruce Caballero, 26°31′S, 053°59′W, *F. O. Zuloaga et al. 5560* (MO, SI); Parque Prov. Moconá, 27°08′S, 053°53′W, *J. Daviña et al. 206* (CTES, G); Intersección rte. 20 y 17, 30 km hacia B. de Irigoyen, 26°21′S, 055°53′W, *M. E. Múlgura et al. 1851* (MO, SI). BOLIVIA. **Santa Cruz:** Chiquitos, Santiago de Chiquitos, Serranía de Santiago, 18°40′S, 059°15′W, *F. Mamani & A. Jardim 1281* (MO, USZ); Nuflo de Chavez, Las Trancas, Lomerio, 16°32′45″S, 061°50′21″W, *A. Jardim 1924* (F, MO, NY, USZ); Lomerio, 12 km al N de Las Trancas, 16°31′13″S, 061°50′47″W, *F. Mamani 584* (LPB, MO, NY, USZ). BRAZIL. S. Salvador, Montenegro, *A. Sehnem 3747* (B). **Bahia:** estr. de Ribeirão do Largo para Nova Brasilia Km. 12, 15°31′20″S, 040°41′11″W, *A. M. V. de Carvalho 6921* (NY); Ilhéus, CEPEC, Ilhéus–Itabuna (BR 415) Km. 22, *J. L. Hage et al. 2142* (G); Almadina–Ibatupã rd., Km. 5.3, then lt. 7.9 km on Serra dos Sete Paus Rd., 14°44′11″S, 039°41′57″W, *W. W. Thomas et al. 11447* (NY). **Espírito Santo:** Serra do Caparaó, 20°21′S, 041°51′W, *A. Chase 9631* (GH, MO, US). **Goiás:** Goiabeira–Annapolis, 16°25′14″S, 049°00′40″W, *A. Chase 11517* (GH, US). **Mato Grosso do Sul:** Aquidauana, 20°26′02″S, 055°45′05″W, *A. Chase 11060* (GH, MICH, US). **Minas Gerais:** *A. F. Regnell s.n.* (US); Lavras, 21°14′43″S, 044°59′59″W, *A. Chase 8801* (GH, US); Juiz de Fora, 21°45′40″S, 043°21′23″W, *A. Chase 8618* (GH, US); outskirts of Realeza, jct. BR-116 & BR-262, 20°10′S, 042°10′W, *A. Gentry et al. 49696* (MO); ca. 20 km E of Diamantina, *H. S. Irwin 27581* (NY); Lagoa Santa, 19°37′38″S, 043°53′23″W, *J. E. B. Warming 1159* (C); Caldas, Serra da Cidade, *S. E. Henschen 639* (UPS); Santa Luzia, Faz. Chicaca, *V. Assis 191* (GH); Viçosa, State Agric. School, *S. I. Howard 2276* (NY, TEX). **Paraná:** Serra do Mar, Viaduto dos Padres, *A. C. Cervi 1974* (CTES); Salto Iguassú, *B. Rambo 53616* (B); Capoeira, *G. Hatschbach 45793* (BR, G); Cerro Azul, Mato Preto, *G. Hatschbach 47634* (MO); Rio Piedade, *J. M. Silva & C. Garcia 1944* (C, G, HBG, MO); Curitiba. Morro Grande, *G. Hatschbach 43615;* Laranjeiras do Sul, Passinho, *G. Hatschbach 36609* (GH, HBG, MO, US); Astorga, *N. Imaguire 1838* (US); vic. Rio Branco do Sul, *J. C. Lindeman & J. H. de Haas 5230* (NY, U, US); Morretes, Véu de Noiva, *J. M. Silva & J. Cordeiro 51* (C, CAS); Iguacu falls, 25°42′00″S, 054°26′00″W, *L. B. Smith 15012* (GH, US); Bocaiúva do sul, Estr. Ribeira, Serra do Santana, *O. S. Ribas 2227* (C, G, HBG); *P. Dusén 16291* (GH, US); *R. Reitz 12078* (GH, US). **Rio de Janeiro:** Rio de Janeiro, Sep. 1836, *Gardner 49* (BM); Rio de Janeiro, foot of the Gavia Mtns., *Gardner 49* (BM); Rio Janeiro, 1837, *Gardner 49* (K); about Rio, *Gardner 49* (K); Teresópolis–Além Paraiba, Km. 38, 22°05′S, 042°48′W, *A. Gentry et al. 49704* (MO); Brasilia, *C. Martius s.n.* (M); Rio de Janeiro, 22°54′10″S, 043°12′27″W, *L. Riedel & B. Luschnath 718* (NY, US); Therezopolis [Teresópolis], *L. H. Bailey & E. Z. Bailey 1287* (BH); Tijuca, *P. Dusén s.n.* (GH); Brasilia, *Ph. V. Lützelburg 25* (M); N. Friburgo, *P. Capell s.n.* (MA). **Rio Grande do Sul:** Excolonia Santo Angelo, 28°17′57″S, 054°15′47″W, *C. A. M. Lindman 1141* (GH, MO, S, UPS, US); Butterberg, P. Montenegro, *B. Rambo 47127* (B); Alto Feliz, *B. Rambo 249* (B); Est. Silvucultura, Santa Maria, *Camargo 60359* (B). **Santa Catarina:** Piratuba, Cascata do Monje, 27°24′39″S, 051°46′16″W, *A. Krapovickas 43996* (F, GH); Tijuca [Tijucas], 27°14′29″S, 048°38′01″W, *A. F. M. Glaziou 3990* (C, P); Apr. 1889, *E. Ule s.n.* (HBG); 27°11′37″S, 051°29′41″W, *P. Dusén 11893* (G, GH, MO, S, US); *R. Reitz 2679* (B, NY); *R. Reitz & R. M. Klein 2335* (B, NY, US); Formosa do Sul, estrada para Jordaninho, *G. F. Árbocz 1063* (F); Rio Canoas, Itajaí, *P. R. Reitz 5164* (US); Estr. Dona Francisca, Joinville, *P. R. Reitz & Klein 6549* (US); Estr. Doña Francisca, Joinville, *P. R. Reitz & R. M. Klein 16785* (B, GH, L, NY, US). **São Paulo:** Judaiaí, IAC, Banco de Germoplasma, *L. C. Bernacci 2178* (F); Capital Vila Cerqueira Cesar, *F. C. Hoehne s.n.* (SPF); Mairiporã: 24.7 km S along rd. from Nazaré Paulista, 23°19′S, 046°35′W, *G. Eiten & L. T. Eiten 1844* (GH, NY, US); Socorro, bairro dos Domingues, próx. sítio Beija–Flor, *M. Groppo 388* (K, SPF); Atibaia, Serra de Itapetininga, estr. a Pedra Grande, *M. A. Farinaccio et al. 582* (SPF); Aguas da Prata, 21°52′S, 047°20′W, *A. B. Martins 31409* (SPF); Itararé, Itararé–São Judas, Km. 28, *P. H. Miyagi et al. 412* (SPF); Aguas da Parta, ca. 500 m do Distr. de São Roque da Fartura, 21°51′S, 046°45′W, *V. C. Souza et al. 5001* (SPF); Pr. Jaraguá, *W. Hoehne 11057* (IAC). CARIBBEAN ISLANDS. **Cuba:** San Juan Mtns., Siguanea, El Junco, 1–20 July 1950, *R. A. Howard et al. 163* (GH); Cienfuegos, Belmonte, Soledad, Cienfuegos, 22°07′19″N, 081°21′43″W, *J. G. Jack 6316* (F, US). **Dominican Republic:** *S. Krosnick 591* (JSBD, MO). **Haiti:** Pétionville, 18°30′45″N, 072°17′07″W, *E. C. Leonard 4882* (B, NY, US); vic. Ennery, Dept. 'L'Artibonite, 19°29′N, 072°29′W, *E. C. Leonard 9465* (F, GH, US). **Jamaica:** Hanover, *L. L. Clarkson & W. J. Kress 75-282* (DUKE). COLOMBIA. **Antioquia:** Hatillo, 06°25′N, 075°24′W, *Daniel 941* (US); Salamina, *F. C. Lehmann 4723* (B, F, K, MO, US); vic. Villa Arteaga, *F. Sierra & F. A. Barkley 18C634* (B, US); Cañasgordas, *J. Santa & J. Brand 773* (MO, NY); Amalfi, rd. to Medellín, 1 km N of rd. to Anorí, 06°50′N, 075°09′W, *J. M. MacDougal et al. 4065* (GH, HUA, MO, US); Cordillera Central

Antioquia, vic. Medellín, *R. Perdromo 10* (GH, US); Nariño, Termales "Espíritu Santo," 05°34′N, 075°03′W, *R. Fonnegra et al. 5181* (GH, HUA, LL, MO, U, US); San Luis, Cañón del Río Claro, 05°53′N, 074°39′W, *A. Cogollo 1839* (JAUM, MO); Santa Bárbara, 05°48′51″N, 075°35′30″W–05°51′37″N, 075°33′37″W, *F. W. Pennell 10895* (GH, US); 5 km SO de Santa Barbara, *L. K. Albert de Escobar & U. Lucia 390* (LL); Zaragoza, Quebrada Cogüí, 2 km antes de la desembocadura del Río Mata en el Río Porce, *F. J. Roldan & R. Fonnegra G. 2704* (MO, NY). **Caldas:** entre La Felisa y Filadelfia, *L. K. Albert de Escobar & J. Brand 2058* (MA); San Pelegrino–Arauca, Km. 5, *L. K. Albert de Escobar 417* (TEX, U). **Chocó:** Riosucio, Serranias del río Cacarica, vic. desembocaura en el río Atrato, *R. Romero 6347* (F, GH, MO, NY). **Cundinamarca:** Hacienda El Cuchero entre Tocaima y Pubenza, *E. P. Killip & A. Dugand 38368* (GH, US); Caparrapi, Hacienda Saldaña, *H. Garcia-Barriga 7729* (GH, MA, US); Santandercito, *L. Uribe 2511* (MA); hwy. above Tocaima, *O. Haught 6396* (US); La Esperanza, 05°10′N, 074°41′W, *W. A. Archer 3284* (GH, NA, US). **La Guajira:** Chingolita, 3 leguas Ede Carraipia, *R. Romero 4404* (NY). **Magdalena:** "Cincinnati," lower slopes of Mt. San Lorenzo, near Santa Marta, 01°06′40″N, 074°05′33″W, *W. E. Seifriz 15* (GH, US); Santa Marta, banks of River Don Diego, *H. H. Smith 2780* (NY). **Risaralda:** Belen de Umbria, Caldás, Belén, 05°12′13″N, 075°52′14″W, *F. W. Pennell 10613* (GH, US). **Santander:** Río Suratá valley, El Jaboncillo–Suratá, 07°19′38″N, 073°01′00″W–07°22′39″N, 072°58′36″W, *E. P. Killip & A. C. Smith 19044* (GH, NY, US); San Juan Valley (Camp IV), 06°30′N, 074°14′W, *O. Haught 1768* (GH, US); Bucaramanga, 07°07′51″N, 073°06′33″W, *E. P. Killip & A. C. Smith 19340* (GH, US); Charta, 07°17′03″N, 072°58′11″W, *E. P. Killip & A. C. Smith 19037* (GH, NY, US); Surata, 07°22′10″N, 072°59′14″W, *E. P. Killip & A. C. Smith 16477* (A, GH, NY, US). **Tolima:** El Libano, *H. García-Barriga 12230* (GH, US); Libano, 04°55′27″N, 074°57′28″W, *F. W. Pennell 3424* (GH, MO, NY, US); Fresno regíon de "Cerro Azul" hacienda de "El Diamante," *H. García-Barriga 08265* (US). **Valle del Cauca:** Piedra de Moler, 04°42′27″N, 075°51′04″W, *E. André 2418* (K); Cisneros, 04°49′21″N, 076°47′20″W, *E. P. Killip 5371* (GH, US); near Palmira, 03°31′58″N, 076°13′47″W, *F. W. Pennell & E. P. Killip 6167* (GH, NY, US); Dagua, *E. P. Killip 11443* (GH, NY, US); La Palle–Zarzal, Hacienda El Medio, *F. A. Silverstone-Sopkin & N. Paz 3189* (MO); *P. Silverstone-Sopkin et al. 4044* (MO); Las Delicias NW of Restrepo Valle, *Bridgeman 212* (K, US); Cisneros, *E. P. Killip 35528* (GH, US). COSTA RICA. **Alajuela:** *V. J. Dryer 763* (F); Zarcero, Guadalupe, 10°10′48″N, 084°24′36″W, *A. Smith 2293* (NA, US); region of Zarcero, 10°10′48″N, 084°23′24″W, *A. Smith A587* (EAP, F). **Cartago:** El Guarco, ca. 13.4 km S of San Isidro de Tejar, lower slopes of Talamancas, 09°46′12″N, 083°59′24″W, *J. M. MacDougal 685* (DUKE). **Guanacaste:** Abangares, upper San Gerardo Valley, 5 km N of Monteverde, 10°21′N, 084°48′W, *W. Haber & W. Zuchowski 9536* (MO). **Heredia:** vic. of Bajo La Hondura, rd. btw. Paracito & Río Claro, 10°03′36″N, 083°58′48″W, *T. B. Croat 44486* (MO). **Limón:** Pococí, Parque Nac. Braulio Carrillo, cuenca del Sarapiquí, 10°08′55″N, 083°56′55″W, *A. Rodriguez et al. 5186* (MO). **Puntarenas:** 10°20′N, 084°50′W, *W. A. Haber 3884* (MO); Monteverde, upper San Luis River valley, 10°20′N, 084°50′W, *W. A. Haber ex E. Bello 3932* (DUKE, MO); camino hacia la R. B. de Monteverde, 10°20′00″N, 084°49′30″W, *A. Estrada 2437* (F). **San José:** 09°32′24″N, 083°55′48″W, *M. Valerio 178* (BR, CR, F); La Palma, 10°03′00″N, 083°58′48″W, *Tonduz 7426* (US); Vazquez de Coronado, Parque Nac. Braulio Carrillo, Cuenca del Sarapiquí, riberas del Río Sucio, 10°09′00″N, 083°57′00″W, *A. Rodríguez G. & V. H. Ramírez 5110* (G); La Palma area, NE of San Jeronimo, above the La Hondura valley, 10°01′48″N, 084°00′00″W, *W. C. Burger & G. Visconti 10231* (F); below La Palma, along the Río Claro trail to Guapiles, 10°01′48″N, 083°58′48″W, *W. C. Burger 4152* (F); environs de San José, 09°55′48″N, 084°04′48″W, *H. Pittier 16675* (CR). ECUADOR. **El Oro:** Piñas–Santa Rosa rd., above El Placer, 03°37′S, 079°49′W, *G. Harling et al. 15568* (AAU, GB). **Loja:** Alamor–Cazaderos rd., El Limo, 03°39′S, 080°09′W, *G. Harling & L. Andersson 17839* (AAU, GB). **Los Ríos:** Río Palenque Biol. Station, 00°35′S, 079°22′W, *C. H. Dodson et al. 5240* (GH, RPSC, SEL, US). **Pichincha:** 20 km W of Santo Domingo de los Colorados, 00°14′38″S, 079°19′26″W, 1 Nov. 1961, *P. C. D. Cazalet & T. D. Pennington 5240* (B, K, NY, UC). GUATEMALA. **Chiquimula:** along Río Tacó, Chiquimula–Montañ Barriol, 3–15 mi. NW of Chiquimula, 14°49′50″N, 089°34′01″W, *J. A. Steyermark 30630* (F). **Jalapa:** mtns. about Chahuite, NW of Jalapa, 14°40′26″N, 090°02′48″W, *P. C. Standley 77481a* (F). **San Marcos:** near & above El Porvenir, 14°58′39″N, 091°56′07″W, *J. M. MacDougal et al. 6238* (MO). **Santa Rosa:** Cuajiniquilapa, 14°16′38″N, 090°17′55″W, *E. T. Heyde & E. Lux 6142B* (GH, US); Guachipilín, 14°09′37″N, 090°01′25″W, *E. T. Heyde & E. Lux 6141* (B, G, GH, US). **Sololá:** finca Santo Thomas Pachuj, Patulul–Lucas Toliman, 14°36′35″N, 091°06′09″W, *H. Forther 10251* (MSB). HONDURAS. **Lempira:** Guatán–Cuábanos, faldas Montaña Puca, *A. Molina 12920* (EAP, F). NICARAGUA. **Jinotega:** El Recreo, 4 km N de Santa Gertrudis, 13°13′N, 085°53′W, *P. P. Moreno & J. C. Sandino 7907* (MO). PANAMA. **Chiriquí:** Fortuna project Dam under construction, SE of AOKI camp, 08°45′N, 082°16′W, *J. P. Folsom et al. 8183* (TEX); Phyllo del Cerro Fortuna, 08°45′N, 082°15′W, *M. D. Correa et al. 2966* (MO, PMA); 12 km N of Los Planes de Hornito, IRHE Fortuna Hydroelectric Project, 08°43′N, 082°14′W, *S. Knapp & M. Vodicka 5500* (MO). **Coclé:** Cerro Pilón, El Valle, 08°38′16″N, 080°06′18″W, *J. A. Duke & B. R. Lallathin 15023* (MO); trail from above El Copé to Río Blanco del Norte, 08°41′00″N, 080°35′54″W–08°43′00″N, 080°36′24″W, *S. Knapp et al. 3667* (MO); N slopes of Cerro Caracorral, 08°37′31″N, 080°06′58″W, *J. M. MacDougal & J. Lezcano 6259* (MO, PMA); ca. 3.2 km (air) NE of church at El Valle, 08°37′35″N, 080°06′57″W, *J. M. MacDougal & J. Lezcano 6269* (MO, PMA). **Veraguas:** past Escuela Agrícola on rd. to Calovebora; 08°32′N, 081°07′W, *C. Hamilton et al. 1260* (MO); forests above Primero Brazo del Río Santa Maria, just W of Santa Fé, 08°34′N, 081°07′W, *S. Knapp & R. Dressler 5383* (MO); Santa Fe, Primer Brazo del Río Ulabá, 08°33′N, 081°07′W, *J. E. Aranda et al. 2805* (PMA, SCZ). PARAGUAY. **Alto Paraná:** Est. Río Bonito, 25°37′55″S, 054°48′17″W, *E. M. Zardini & L. Guerrero 44619* (AS, MO); Viv. Ftal Itaipú, Orilla de bosque, 8 Mar. 1979, *Itaipú Binacional 208* (MO); Escuela Técnica Forestal, Puerto Pres. Stroessner, Km. 12, *F. J. Fernández Casas & J. Molero 5663* (MA, MO, NY); Río Alta Parana, *K. Fiebrig 6027* (B, BM, E, G, GH, P, US); Escuela Tecnica Forestal Km. 12 Puerto Pres. Stroessner, *M. Bernardi 18893* (NY); Río de La Plata, 1854, *E. Palmer s.n.* (US); Chemin, C. F. A. P., Puerto Stroessner, Km. 12, *L. C. Stutz de O. 2107* (NY). **Amambay:** Est. Carmen de la Sierra, *N. Soria 4379* (MA, MO). **Caaguazú:** Villa Rica [Sierra de Villa Rica], 25°36′S, 055°58′W, *P. Jörgensen 3792* (C, CAS, DLY, F, GH, MO, NY, PH, US). **Caazapá:** Natl. Park Caaguazú, 26°05′49″S, 055°28′58″W, *E. M. Zardini & A. Benítez 47522* (AS, MO, NY). **Central:** Par Centralis, Regio lacus Ypacaray; "Cordillera de Altos," 25°17′S, 057°20′W, *E. Hassler 11531* (B, BM, C, E, F, G, GH, K, L, MO, NY, US, WIS); Ypoá, Tacuara, 4 km NW of Cerro Pé, 25°38′S, 057°28′W, *E. Zardini & L. Guerrero 33371* (AS, MO, US); Tavarory, 2.5 km from admin. toward Arroyo Abai, 25°30′S, 057°30′W, *E. Zardini & T. Tillería 29427* (AS, MO); 1 km W from entrance to Tavarory, 25°30′S, 057°30′W, *E. M. Zardini & L. Guerrero 31572* (AS, CAS, MO); 2.5 km W from entrance to Tavarory, 25°30′S,

057°30′W, *E. M. Zardini & T. Tillería 31763* (AS, BH, CU, MO); Itá Enramada., *M. M. Arbo et al. 1677* (CTES); *T. M. Pedersen 5264* (C, GH, US); San Lorenzo, 25°20′S, 057°32′W, *W. A. Archer 4761* (NA); San Lorenzo del Campo Grande, Orslasde montes Laurelty, *T. Rojas 9367* (LIL). **Concepción:** Est. Santa Maria de la Sierra, 22°43′48″S, 057°27′07″W, *E. M. Zardini & L. Guerrero 41577* (AS, MO); Est. Primavera–Vallemi, 22°24′07″S, 057°37′33″W, *E. M. Zardini & L. Guerrero 57260* (MO); Parque Nac. San Luis de la Sierra, 22°40′21″S, 057°20′29″W, *E. M. Zardini & M. Vera 40947* (AS, MO); Río Apa & Río Aquidaban, *K. Fiebrig 4108* (B, E, G, K). **Cordillera:** San Bernardino, Costa del Lago Ipacaray, *C. L. Quarin et al. 1561* (CTES); Tobatí "Ybytú Silla" mesa S area, 25°12′S, 057°07′W, *E. Zardini & R. Velázquez 27278* (FCQ, MO); betw. Emboscada & Nueva Colombia, 25°07′S, 057°19′W, *E. M. Zardini & L. Guerrero 35902* (AS, MO); San Bernardino, *T. Rojas 13269* (CAS, LIL). **Guairá:** Cordillera de Ybytyruzú, rd. to Cantera Jhú, 25°48′S, 056°20′W, *E. Zardini & R. Velásquez 14513* (FCQ, MO); cumbre del Cerro Acati, 25°55′S, 056°15′W, *I. Basualdo 002421* (MO, TEX); cumbre del Cerro Acati, 25°55′S, 056°15′W, *M. Ortiz 001185* (MO); Ybyturuzú [Ybytyruzú], en la cumbre del Cerro Acati, 25°55′S, 056°15′W, *N. Soria 3491* (FCQ, MO). **Itapúa:** Est. Parabel, *S. Keel 1900* (MO); Dpto. Cantera, Colonia Alborada, *J. E. Montes 3279* (K). **Paraguarí:** Natl. Park Ybycu'í, 26°01′S, 056°46′W, *E. M. Zardini & L. Guerrero 31039* (F, MO, NY, PY); Macizo Acahay, 25°54′S, 057°09′W, *E. M. Zardini & C. Velásquez 9235* (MO, PY); Cordillera de Altos, 25°30′S, 057°09′W, *K. Fiebrig 426a* (B, E, F, G, L); Cordillera de Altos, 25°30′S, 057°09′W, *K. Fiebrig 194* (B, E, G). **San Pedro:** Alto Paraguay, Primavera, *A. L. Woolston 1206* (C, GH, U, US). URUGUAY. **La Valleja:** 34°22′12″S, 055°13′30″W, *W. G. Herter 2606* (B). VENEZUELA. 1879, *Ernst s.n.* (B); 1879, *E. M. Reineck s.n.* (HBG). **Falcon:** Parque Nac. Cueva de la Quebrada el Toro, *G. L. Sobel & J. J. Strudwick 2064* (NY); *J. Steyermark 99246* (NY, US). **Miranda:** La Mocca [La Moca], 10°22′N, 066°36′W, *Eggers 13530* (C).

2. Passiflora cervii M. A. M. Azevedo, Brittonia 60(4): 310–312. 2008. TYPE: Brazil. Minas Gerais: Viçosa, *s. coll. s.n.* (holotype, VIC not seen). Figure 9.

Vines moderately to densely villous throughout; stems 3-angular, striate. Stipules (4.6–)4.9–5.6(–6.1) × (0.3–)0.4(–0.5) mm, narrowly triangular, sparsely pubescent abaxially; petioles (9–)12–18(–23) mm; leaf laminas (5–)5.7–6.5(–7.4) × (4.9–)5.2–5.8(–6.1) cm, broadly obovate, cordate at the base, densely villous abaxially with trichomes 0.4–0.5 mm, sparsely villous adaxially with trichomes 0.3–0.5 mm, 3-lobed, the lateral lobes acute to obtuse, the central lobe reduced and obtuse; angle between lateral veins (45°–)48°–56°(–58°). Peduncles (23–)27–49(–67) mm, slender, solitary; floral stipes 3.1–3.6 mm, to ca. 8.1 mm in fruit. Flowers (26–)27–29(–31) mm diam., white to pale cream; sepals (12.7–)15.6–17.3(–19.8) × (1.9–)2.6–3.4(–4.3) mm, narrowly triangular, apex acuminate, sparsely hirsute outside; petals (8.6–)10.2–11(–13.6) × (1.2–)2.1–2.3(–2.6) mm, linear to narrowly triangular, ca. 2/3 as long as the sepals, apex acute; corona filaments in 1 series; filaments 30 to 32, (8.3–)9.6–10.8(–11.7) mm, shorter than petals; operculum (1.9–)2–2.3(–2.6) mm; androgynophore 5.8–8.1 mm; stamens with filaments 4.4–5.1(–5.5) mm; anthers 3.2–3.7(–3.9) × (1.2–)1.4–1.5 mm; ovary 3.1–4.5 × 1.7 mm, ellipsoid to obovoid, hispid to minutely puberulous; styles (3.3–)3.5–4.1(–4.6) mm; stigma 1–1.1 mm diam. Fruits ca. 44 × 15 mm, obovoid or fusiform, glabrous to subglabrous, color unknown; seeds 1.8–2.5 × 1.2–1.5 mm, transversely sulcate with 5 or 6 sulci, the sculpturing of the ridges unknown to us.

Phenology. Flowers of *Passiflora cervii* have been observed from October to April. Fruits have been documented from February to June and from October to December.

Distribution and habitat. *Passiflora cervii* is restricted to southeastern Brazil and has been collected from the states of Minas Gerais, São Paulo, Pará (João Batista Fernandes da Silva, pers. comm., cf. Fig. 9), Paraná, Santa Catarina, and Rio Grande do Sul (Fig. 5) in both montane rainforest and coastal forest. Specimens of *P. cervii* were little available during this study, so Figure 5 includes additional distribution records taken from the author of the species (Milward-de-Azevedo, 2008; Milward-de-Azevedo et al., 2012).

Local names. Maracujazinho (Milward-de-Azevedo, 2008; Santa Catarina, Brazil).

Discussion. *Passiflora cervii* is closely related to *P. capsularis*, *P. cisnana*, and *P. rubra*. The most important character to distinguish the three is the ovary indumentum, which is glabrous or minutely puberulous in *P. capsularis*, hispid to minutely puberulous in *P. cervii*, and usually densely white to brown hirsute in *P. cisnana* and *P. rubra*. *Passiflora cervii* can also be distinguished by its broadly obovate leaves, ligulate corona filaments, oblate and spheroid pollen grains, and by its restricted geographic distribution (Milward-de-Azevedo, 2008).

Passiflora cervii was recognized to be sympatric with *P. capsularis* and allopatric with *P. rubra* (Milward-de-Azevedo, 2008; Milward-de-Azevedo et al., 2012). Indeed, there are some specimens of *P. capsularis* from the south and southeast of Brazil that share the same geographic area with *P. cervii* (e.g., *Gentry 49696* and *Irwin 2276*). We have seen only three specimens of *P. cervii*: one from Minas Gerais, Viçosa, which is the type locality (*Mexía 5402*), one from Paraná (Rio Branco do Sul; *Oliveira 691*), and the other from Rio Grande do Sul (Montenegro; *Sehnem 2430*). These specimens represent almost the complete known geographical range of *P. cervii*. We also have seen several photographs from Pará, Brazil, that appear to be of this species, and the color description of the flower of *P. cervii* is taken from these photographs.

Selected specimens examined. BRAZIL. **Minas Gerais:** Viçosa, rd. to Barroso, Faz. Aguada, 20°45′20″S,

Figure 9. *Passiflora cervii* M. A. M. Azevedo, flowers and leaves in the field, Serra Leste, Serra dos Carajás, Brazil. —A. Leaves with flower starting to close. —B. Flower with leaf. —C. Flower, side view. Scale bars: A = 1 cm; B, C = 0.5 cm. Photographer: A–C, João Batista Fernandes da Silva.

042°52′02″W, *Y. Mexía 5402* (CAS, G, GH, MO, NY, S, US). **Paraná:** Rio Branco do Sul, Lavarinha, Paraná, 25°11′24″S, 049°18′51″W, *P. I. Oliveira 691* (HBG, NY, SP). **Rio Grande do Sul:** S. Salvador, Montenegro, 29°41′59″S, 051°28′46″W, *A. Sehnem 2430* (CAS).

3. Passiflora cisnana Harms, Bot. Jahrb. Syst. 18 (Beibl. 46): 5. 1894. TYPE: Ecuador. Loja "crescit in fruticetis ad Cuesta da Cisna [Cisne]," 1200–1500 m, Nov. 1888, *F. C. Lehmann 4833* (holotype, B†, B photo at F neg. no. 16525!, B photo at F-587795!, B photo at F-666174!, B photo at MO-1680886!; lectotype, designated here, K [barcode] 000036545 image!; isolectotype, NY!). Figures 10, 23B, C.

Vines 2–4 m, densely and softly pubescent; stems 3- or 4-angular. Stipules (2.2–)4.4–5(–7.8) × (0.3–)0.5–0.7(–1) mm, linear to linear-triangular, ± falcate, sparsely pubescent abaxially; petioles (5–)14–20(–33) mm; leaf laminas (3.1–)5.5–6.6(–9.1) × (2.7–)5.4–6.5(–9.5) cm, broadly obovate or rarely depressed obovate, bases deeply cordate, densely hirtellous abaxially with trichomes 0.2–0.9 mm, densely hirsute adaxially with trichomes 0.4–1.1 mm, 2- or 3-lobed, the lateral lobes

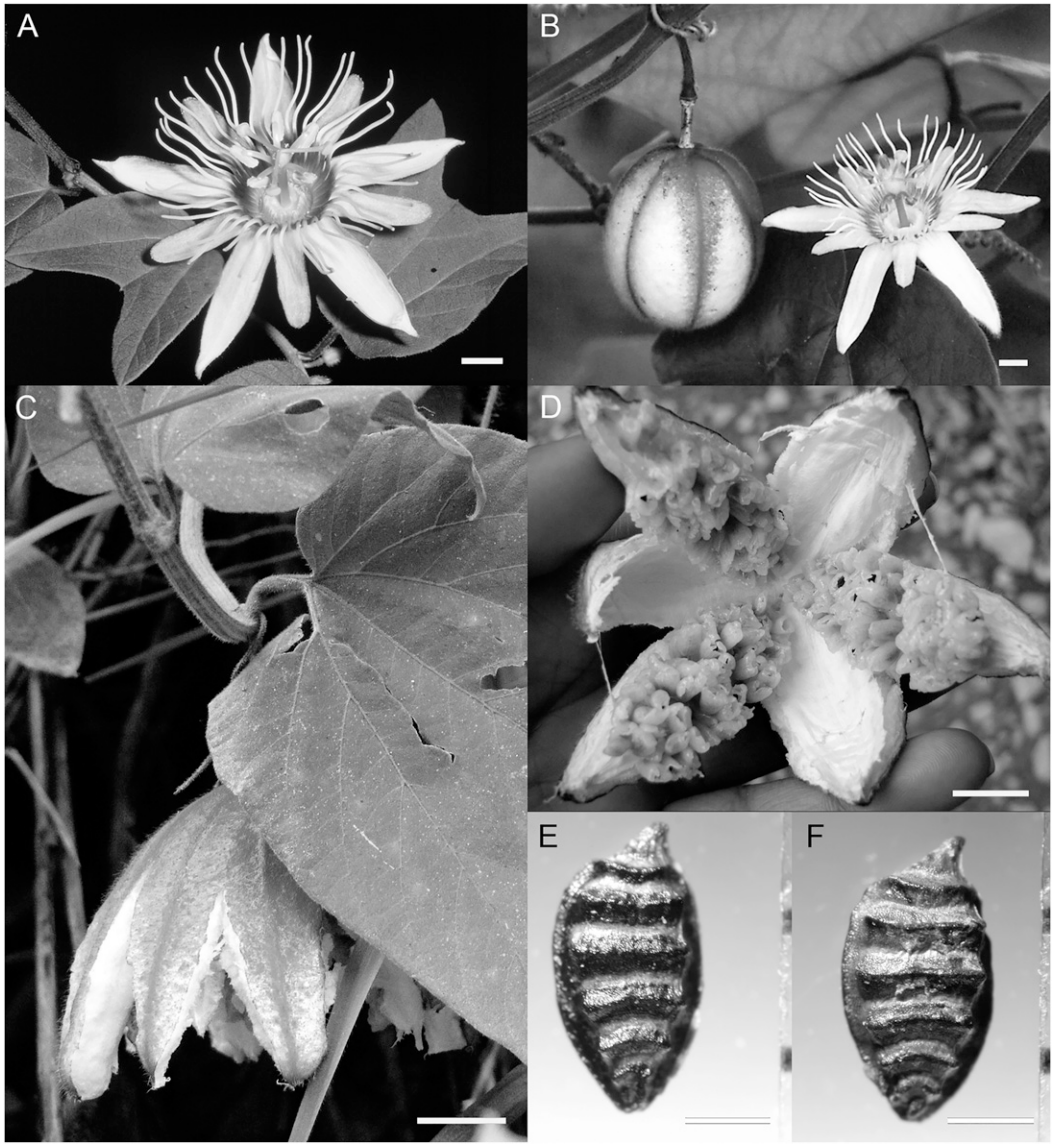

Figure 10. *Passiflora cisnana* Harms. —A. Flower, cultivated by L. E. Gilbert, seed originating from Jaén, Peru (*J. M. MacDougal 430*). —B. Flower and undehisced fruit, cultivated. —C. Dehisced fruit, side view, Peru (*T. E. Boza et al. 2048*). —D. Dehisced fruit showing valves and aril-covered seeds, Peru (*T. E. Boza et al. 2048*). —E. Seed, Venezuela (*W. Diaz 2538*). —F. Seed, Guyana (*D. Clarke 858*). Scale bars: A, B = 0.5 cm; C, D = 1 cm; E, F = 1 mm. Photographers: A, John MacDougal; B, Don Ellison; C–F, Tatiana Boza.

acuminate to acute, or when central lobe is evident obtuse or rounded; angle between lateral veins (32°–)51°–58°(–76°). Peduncles (4–)16–21(–46) mm, slender, solitary or rarely in pairs; floral stipe 1–6.5 mm, to 1.4–7.5 mm in fruit. Flowers 43–45 mm diam., greenish white or pale yellow-green; sepals (10.3–)16.7–18.2(–24.4) × (2.2–)3–3.6(–5.8) mm, narrowly triangular, sparsely hirsutulous outside, apex acute (but acuminate or rounded in coastal Ecuador and northwestern Peru), white or rarely pink at base; petals (5.1–)10.3–11.7(–15.3) × (1.2–)1.9–2.2(–4.4) mm, narrowly oblong or linear to narrowly triangular, ca. 1/2(3/4) as long as the sepals, apex slightly praemorse to obtuse or rounded or less often acute, white; corona filaments in 2 or rarely 1 series; filaments of outer series 32 to 38, (5.4–)10.1–11.1(–15.8) mm, shorter than petals or intermediate between sepals and petals, filiform, red, pink, or purplish at base, cream to white above; when exceptionally present, filaments of inner series (1.2–)1.8–2(–2.5) mm, shorter than outer series; operculum (0.9–)

1.3–1.5(–2.2) mm; androgynophore 5.1–9.9 mm, green; stamens with filaments (2.7–)3.8–4.2(–4.8) mm; anthers (2.2–)3.3–3.6(–5.3) × (0.8–)1.2–1.3(–1.7) mm; ovary 2.1–4 × 1.1–3 mm, ellipsoid, densely hirsute with trichomes often drying brownish; styles (1.9–)2.9–3.3(–4.6) × 0.2–0.3 mm; stigma (0.6–)0.9–1.1(–1.6) mm diam. Fruits (21–)36–44(–63) × (7–)14–19(–39) mm, subglobose, ellipsoid to obovoid, or abruptly acute at apex, often slightly hexagonal, hirsute or rarely glabrous, reddish brown, dark purplish red, or red, often somewhat white or cream between the ridges; seeds (1.9–)2.8–3.1(–3.7) × (1.3–)1.6–1.8(–2) mm, transversely sulcate with 6 or 7(8) sulci, either lacking a distinct projection or with a reduced one, < 0.54 mm.

Phenology. Flowers of *Passiflora cisnana* have been observed in January, February, and from September to November. Fruits were observed in January, from March to July, and in December.

Distribution and habitat. *Passiflora cisnana* is known from Colombia, Venezuela, Guyana, French Guiana, and northeastern and eastern Brazil (Ceará, Maranhão, Minas Gerais, Pernambuco, Rio de Janeiro) to Bolivia, Peru, and Ecuador (Fig. 5). It has been collected from mountains and in surrounding lowland Amazonian rainforest, from 150 to 3000 m in elevation.

Local names. Mazomanchachi (*Boza & Chambi 2048*; Cusco, Peru).

Discussion. The holotype for *Passiflora cisnana* was destroyed at Berlin during World War II. Isotypes were found at NY and K. The K duplicate is designated as lectotype because it is more representative, and it has well-preserved flowers.

Passiflora cisnana was originally described by Harms in 1895 as a species from Loja, Ecuador, distributed from 1200 to 1500 m altitude. Later, Killip (1938) would place *P. cisnana* in synonymy under *P. rubra*, assessed by him as simply a form of that species from Ecuador with denser indumentum and smaller leaves.

Sterile collections of *Passiflora cisnana* and *P. rubra* are indeed difficult to distinguish. However, there are differences in sepals, petals, corona filaments, and ovary shape between the two. The color of the corona filaments differs between the species and appears to be a very dependable character to distinguish them: the filaments are red, pink, or purplish at the base, and cream to white above in *P. cisnana*, compared to red, pink, or purplish dots over the entire filament length and usually darker toward the base in *P. rubra*. *Passiflora cisnana* is characterized by having sepals with apices that are acute (or rarely acuminate in coastal Ecuador and northwestern Peru), and by petals that are about 1/2 as long as the sepals (or more, up to 3/4, in northwestern Peru, coastal Ecuador, southwestern Colombia, coastal Venezuela, and Guyana), and by petal apices that are slightly praemorse to obtuse or rounded and sometimes acute (northwestern Peru and coastal Ecuador). By comparison, in *P. rubra* the sepals have slightly acuminate to slightly rounded apices, the petals are more than 3/4 as long as the sepals (but ca. 1/2 as long in material from the Bahamas, Guadeloupe, Dominican Republic, and Puerto Rico), and the petals may have acute or sometimes slightly praemorse to rounded apices. The corona of *P. cisnana* usually has two series of filaments (but *Lasser 1552* and *Knapp & Mallet 2838* has only one series), with the length of the outer series shorter than the petals or intermediate between the sepals and petals. By contrast, *P. rubra* has one or two series of corona filaments, with the outer series intermediate between sepals and petals or as long as the petals. The ovary shape is also different: it is ellipsoid in *P. cisnana* and obovoid to subglobose in *P. rubra*. *Passiflora cisnana* has a wide distribution in South America, while *P. rubra* is restricted to the Caribbean Islands.

Selected specimens examined. BOLIVIA. *M. Bang 2836* (B, BM, CTES, F, G, GH, K, MICH, MIN, MO, NY, PH, S, US, W). **Chuquisaca:** Hernando Siles, SO de Monteagudo, 19°35′22″S, 064°05′19″W, *J. A. Peñaranda et al. 315* (HSB, MO); Toma de Agua del Río Limon, Monteagudo, 19°45′S, 063°57′W, *K. Wendelberger et al. 397* (MO); Serranía Los Milagros, Guayabillar–Cañon Largo, 20°19′21″S, 064°02′00″W, *M. Serrano et al. 7030* (HSB, MO); Luis Calvo, Abra del Incahuasi, 19°48′52″S, 063°43′10″W, *A. Llully et al. 628* (HSB, MO, TEX); Ticucha, aprox. 12 km al NO de Ticucha, Alto Iñao, 19°34′S, 063°54′W, *J. Gutierrez et al. 331* (MO, NY); Sud Cinti, Orocote, NO de Orocote entre los rios Limonal y Cochayo, 20°47′S, 064°21′W, *R. Lozano et al. 1177* (MO, NY); Tomina, aprox. 3 km de Las Casas, sector de Pampillos, 19°19′42″S, 064°06′58″W, *J. Gutiérrez et al. 1219* (LPB, MO, NY); aprox. 50 min. de Las Casas, trayecto a Llantoj, 19°18′48″S, 064°06′58″W, *J. Gutiérrez et al. 1042* (JPB, LPB, MO, NY); Llantoj, aprox. a 1 hr. bajando de Abra Santa Cruz, 19°18′57″S, 064°05′15″W, *J. Gutierrez et al. 1089* (MO, NY); Monteagudo, 64 km hacia Sucre, 19°30′S, 064°10′W, *S. G. Beck 6367* (LPB, M, MO). **La Paz:** La Paz–Caranavi, 15°59′56″S, 067°35′02″W, *T. E. Boza & J. Uzquiano 2109* (MO); La Paz–Chulumani, *L. K. Albert de Escobar 1302* (QCA, TEX); Abel Iturralde, Río Tuichi, 14°18′S, 068°35′W, *D. Lara 290* (MO); Franz Tamayo, 15 km rio arriba de la Hacienda Ubito, 14°24′S, 068°27′W, *M. Kessler 3964* (LPB); Parque Nac. Madidi, NO de Apolo, 14°33′39″S, 068°41′24″W, *L. Cayola 1550* (BOLV, CTES, HSB, LPB, MO, NY); Loayza, before summit on Miguillas–La Plazuela rd., 16°28′S, 067°22′W, *L. J. Dorr et al. 6923* (LPB, MO, NY); Muñecas, 1.4 km NO de Camata, 15°14′46″S, 068°45′31″W, *A. Fuentes et al. 10631* (BOLV, LPB, MA, MEXU, MO, NY, USZ); Nor Yungas, 19 km NE of Chuspipata, 16°13′S, 067°46′W, *A. Gentry & J. Solomon 44392* (LPB, MO, NY); Milluguaya, 16°21′37″S, 067°35′51″W, *O. Buchtien 636* (E, GH, HBG, NA, NY, US); Polo-Polo by Coroico, 16°11′20″S, 067°43′37″W, *O. Buchtien 3852* (GH, US); Polopolo by Coroico, 16°11′00″S, 067°44′00″W, *O. Buchtien 3872* (GH, US); Coroico–Trinidad

9 km, 16°08′S, 067°42′W, *J. P. Schmitt et al. 371* (LPB, MO); Caranavi–Alto Beni ca. 8 km, *J. R. I. Wood & D. Mondaca 14553* (K, LPB); Yolosa–Coroico 3.4 km, 16°13′S, 067°44′W, *J. C. Solomon 4835* (MO); Coroico, near Hotel Prefectural, 16°11′S, 067°43′W, *J. C. Solomon et al. 12065* (LPB, MO); Coroico–Santa Barbara, 16°10′S, 067°43′W, *M. Delanoy 146* (MO); 16°10′S, 067°43′W, *M. Delanoy 147* (MO); 16°12′S, 067°40′W, *M. Delanoy 176* (MO); valle del Río Unduavi, 16°44′S, 067°24′W, *R. Seidel & E. Vargas 1183* (LPB); 4.5 km S de Coroico, 16°13′S, 067°45′W, *S. G. Beck 17220* (K, LPB, MO, SI, TEX, US, USZ); Caranavi–Coroico 35 km, 16°03′S, 067°41′W, *S. G. Beck 13515* (LPB, TEX); desvio hacia el valle de Huarinillas, 16°12′S, 067°47′W, *S. G. Beck 24604* (LPB); Sud Yungas, Chulumani–Irupana, pasado Chímasi, puente del Río Solacama, 16°25′24″S, 067°29′19″W, *F. Muñoz Garmendia & J. P. Pivel Rainieri 3055* (MA, MO); Yolosa–Coroico 2.4 km, 16°12′S, 067°45′W, *L. Albert de Escobar & J. C. Solomon 4824* (F, HUA, LPB, MA, MO, QCA, TEX); Yuni Grande–Huancallo, Irupana, 16°26′S, 067°27′W, *M. Delanoy 316* (MO); the old electric plant–Irupana, near the river, 16°28′S, 067°26′W, 19 Dec. 2003, *M. Delanoy 312* (MO); 16°28′S, 067°28′W, *M. Delanoy 307* (MO); Uyuca–Duraznuni, Irupana, 16°28′S, 067°25′W, *M. Delanoy 304* (MO); 16°28′S, 067°23′W, *M. Delanoy 290* (LPB, MO); Porotoco–Siquiljara, Irupana, 16°30′S, 067°26′W, *M. Delanoy 287* (MO); Río Blanco–Huancane, Chulumani, 16°19′S, 067°32′W, *M. Delanoy 207* (MO); Ocobaya–Chulumani, 16°25′S, 067°29′W, *M. Delanoy 212* (MO); Las Lomas–San Antonio, Chulumani, 16°23′S, 067°31′W, *M. Delanoy 220* (MO); 16°21′S, 067°31′W, *M. Delanoy 227* (MO); Chulumani–Chimasi, 16°23′S, 067°31′W, *M. Delanoy 236* (MO); Ocobaya–Chicaloma, 16°25′S, 067°29′W, *M. Delanoy 244* (MO); Irupana–Yuni Grande, 16°28′S, 067°26′W, *M. Delanoy 247* (MO); La Florida–Santa Rosa, Yanacachi, 16°21′S, 067°45′W, *M. Delanoy 403* (MO); Chaco–La Florida, Yanacachi, 16°21′S, 067°45′W, *M. Delanoy 418* (MO); Cruz Loma–Coroico, 16°10′S, 067°42′W, *M. Delanoy 7* (MO); Yolosa–Coroico, 16°12′S, 067°43′W, *M. Delanoy 15* (MO); Chicaloma, 16°27′S, 067°29′W, *S. G. Beck 22650* (LPB, MO); Puente Villa–Chulumani, Km. 36, 16°22′S, 067°34′W, *S. G. Beck 21352* (LPB, MO); Chulumani 107 km hacia el NNE, pasando Asunta, 16°04′S, 067°12′W, *S. G. Beck 8553* (HUA, LPB, US); Lomachica–Ocobaya 1.5 km, 16°27′S, 067°27′W, *S. G. Beck 22281* (LPB, MO, NY); Colaya, Ranch Tiempaya, *Y. Mexía 4303* (GH, MO). **Santa Cruz:** Buenavista, 17°35′30″S, 063°44′57″W, *J. Steinbach 8045* (E, G, GH, MO, NY, PH); Japacani, *M. Cárdenas 5914* (US); Andres Ibanez, monumento Natural Espejillos, 17°54′07″S, 063°25′56″W, *A. Molina 457* (MO); Cantón Ayacucho, Parque Natural Espejillos, quebrada Espejillos, O de San José, 17°54′S, 063°26′W, *A. L. Arbeláez et al. 621* (MO, NY); Área Privada Nat. Protegida Arubai, 17°42′04″S, 063°23′47″W, *L. Arroyo et al. 3767* (MO, USZ); La Guardia, 5 km al S, 17°30′S, 063°24′W, *S. G. Beck 23428* (LPB, MO); Chiquitos, Serranía Sunsas, camp. de Bocamina, 17°20′S, 060°45′W, *F. Mamani & A. Jardim 1131* (G, LPB, MO, USZ); Cordillera, Cuevo ca. la planchada de Chevron, 20°26′S, 063°30′W, *A. Jardim & N. Rosas-Hurtado 1555* (MO, USZ); Incahuasi–Prov. Cordillera–Puerto Santa Cruz, *M. Cárdenas 4733* (US); Florida, quebrada El Cañadon, 18°14′22″S, 063°40′46″W, *I. G. Vargas et al. 7172* (MO, USZ); 2 km (air) NW of Bermejo, around Laguna Volcán, 18°07′S, 063°39′W, *M. Nee 46142* (LPB, NY); Ichilo, 15 km SSE of Buena Vista, Estancia San Rafael de Amboro, 17°35′S, 063°36′W, *A. Gentry 74109* (LPB, MO, USZ); 5 km WSW of El Hondo, W of Quebrada La Concha, 17°40′S, 063°29′W, *M. Nee & I. Vargas 44925* (LPB, MO, NY, US, USZ); Nuflo de Chavez, Concepción–San Ignacio 75 km, Palmarito, *S. G. Beck 25771* (LPB); Sarah, Buenavista, 17°27′S, 063°40′W, *J. Steinbach 3295* (G, K, US). BRAZIL. **Ceará:** Maranguapé, serra de Maranguapé, *Z. A. Trinta et al. 1270* (CTES); Maranguape, Pirapora, *H. C. Cutler 8129* (US). **Maranhão:** Alzilandia, Rio Pindare, 03°45′S, 046°05′W, *J. I. Jangoux & R. P. Bahia 342* (NY, US). **Minas Gerais:** Caldas, Rio Pardo, *A. F. Regnell 639* (MO, UPS); Faz. Serra Azul, 3.2 km E of Macarani–Bandeiras rd., ca. 12 km N of Bandeiras, 15°49′31″S, 040°31′21″W, *W. W. Thomas et al. 13689* (NY). **Pernambuco:** Tapera, 07°52′S, 037°52′W, *B. J. Pickel 2625* (US). **Rio de Janeiro:** Rio de Janeiro, 22°54′S, 043°12′W, *J. F. Widgren 117* (S, UPS). COLOMBIA. **Antioquia:** *F. C. Lehmann 3140* (G); Mpio. El Jardín, El Jardín–Los Andes, Km. 6, 05°36′N, 079°49′W, *J. M. MacDougal & F. J. Roldán 3621* (MO, US); San Luis–Río Samaná, Km. 2, El Azuceno, *L. K. Albert de Escobar et al. 1953* (QCA); San Carlos–El Jordán, Km. 11.5, *L. K. Albert de Escobar & F. J. Roldán 8817* (TEX). **Caldas:** Pereira, *B. Tomás 2444* (US); San Jose, Cauca Valley, 05°28′51″N, 075°41′08″W, *F. W. Pennell 10240* (PH, US); Cordillera Central, Río Campoalegro, San Francisco, 05°03′17″N, 075°41′59″W, *F. W. Pennell 10183* (GH, NY, US). **Cauca:** Río Ojar, *F. C. Lehmann 3364* (G, K); *F. C. Lehmann 22894* (G). **Cundinamarca:** Sasaima, Apocentos, *H. García-Barriga 17279* (US); Santandercito, sendero El Pin–La Rapida, *A. L. Uribe 3471* (NY); Cachipay, 05°16′N, 074°34′W, *W. A. Archer 3309* (NA, US); Nocaima, Hacienda Tobia, *H. García-Barriga 10593* (US); San Bernardo, *J. Cuatrecasas 9630* (US). **Magdalena:** Alto Río Frío Cabeceras del Río Congo, Ciudad Antigua, 10°59′N, 074°04′W, *S. Madriñán & C. E. Barbosa 518* (GH). **Putumayo:** Mpio. Mocoa, finca La Mariposa, 01°12′N, 076°38′W, *J. Betancur et al. 4986* (COL, MO). **Quindio:** Salento, 04°38′15″N, 075°34′13″W, *F. W. Pennell 9084* (US); Genova, Vereda El Dorado, 04°03′N, 076°25′W, *G. Arbelaez S. et al. 2760* (MO). **Tolima:** Libano, *H. García-Barriga 12233* (US). **Valle del Cauca:** Cali, *L. K. Albert de Escobar et al. 2504* (HUA, NY); Restrepo, 03°49′32″N, 076°31′31″W, *E. P. Killip 11257* (US); Finca El Porvenir, Toro–San Pacho, Km. 6, 03°18′N, 076°14′W, *P. Silverstone-Sopkin et al. 5830* (MO); Cartago–Alcalá, Alto del Dinde, *J. Cuatrecasas 22892* (F, US); Dagua, carr. vieja Cali–Buenaventura, La Elsa, 03°34′47″N, 076°46′54″W, *S. Hoyos & J. Santa 230* (WIS); 4 km al S de El Cerrito, Hacienda El Milagro y hacienda adyacente, 03°38′22″N, 076°17′40″W, *P. Silverstone-Sopkin & J. E. Giraldo Gensini 6184* (MO); Palmira, Hacienda El Guachal, Caucaseco, 03°26′14″N, 076°31′21″W, *J. E. Ramos & N. Paz 922* (MO); Restrepo, Río Bravo, quebrada La Cristalina, El Pital, 04°00′N, 076°00′W, *W. Devia 1118* (MO); Sevilla, *G. Soto Herrera 923* (US); Sevilla–La Raquelita, quebrada la Raquelita, 04°00′N, 076°00′W, *W. Devia 1069* (MO); Versalles, 04°34′39″N, 076°12′11″W, *M. T. Dawe 839* (K, NY, US); Zarzal, 04°23′54″N, 076°04′38″W, *F. W. Pennell et al. 8541* (GH, US); Río Digua Valley, La Elsa–Río Blanco, *E. P. Killip 34774* (US); Hacienda El Medio, La Paila–Zarzal, 04°19′09″N, 076°04′22″W–04°23′54″N, 076°04′38″W, *P. Silverstone-Sopkin et al. 2573* (MO); carr. vieja Cali–Buenaventura, *S. Hoyos 231* (MA). ECUADOR. **Azuay:** vic. Cumbe, 03°05′S, 079°01′W, *J. N. Rose et al. 22984* (US). **Bolívar:** San Miguel, 01°42′S, 079°02′W, *F. L. Stevens 202* (US); Babahoyo–Guaranda, above Balzapamba, 01°48′S, 079°10′W, *L. B. Holm-Nielsen et al. 23065* (AAU, QCA); Guaranda, Chazo Juan–Chorrera de Moras, Km. 3, 01°23′36″S, 079°08′59″W, *H. Vargas 5029* (MO, QCNE). **Cañar:** Cañar Azuay border, Río Patul, Manta Real near Hacienda Aurora, 02°32′S, 079°30′W, *D. D. Kapan 121* (TEX); valley of Río Cañar, near Abadel, 02°29′18″S, 079°06′20″W, *F. Prieto CP-36* (NY). **Chimborazo:** Huigra, 02°17′S, 078°59′W, *A. S. Hitchcock 20747* (GH, NY, US); Huigra, Hacienda Licay, 02°17′S, 078°59′W, *J. N. Rose & G. Rose 22275* (GH, NY, US); Sibambe, Hacienda La Carmela, 02°15′S, 078°54′W, *M. Acosta-Solis 5325* (F); Río Chanchan near Huigra, 02°18′10″S,

078°59′19″W, *W. H. Camp E-3014* (F, G, GH, K, MO, NY, P, S, UC, US); Alausí, sector Illin., 02°20′45″S, 079°02′53″W, *C. E. Cerón et al. 57436* (MO); Hacienda Licay, near Río Chanchan, N of Huigra, old rd. from Guayaquil to Riobamba, 02°15′S, 078°55′W, *J. F. Smith 2046* (QCA, WIS). **Cotopaxi:** Tenefuerste, Río Pilalo, Quevedo–Latacunga, Km. 52–53, 00°59′N, 079°04′W, *C. H. Dodson et al. 13941* (MO); Latacunga–Quevedo, Finca El Copal, Río Pilatón, above El Tingo, *D. D. Kapan 27* (TEX); *D. D. Kapan 72* (TEX). **El Oro:** Río Pejeyacu, 5.15 km above main rd. Pasaje–Uzhcurumi, on rd. to Chilla, 03°21′S, 079°36′W, *D. D. Kapan 41* (TEX); Paccha–Muluncay, *G. Harling 27061* (GB); 7 mi. E Saracay, 03°36′34″S, 079°53′01″W, *L. K. Albert de Escobar 1357* (QCA); Arenillas–Piñas, Zaracay, 03°37′54″S, 079°52′15″W, *T. C. Plowman 5448* (F, GH); Piñas, El Placer, Reserva Ecol. Buenaventura de la Fundación Jocotoco, 03°39′05″S, 079°47′42″W, *H. Vargas et al. 5299* (MO, QCNE); Portovelo–Río Cabra, passing Minas Nuevas, arriving at Cachicarán, 03°43′S, 079°37′W–03°34′S, 079°38′W, *J. A. Steyermark 54091* (F, US). **Esmeraldas:** Pedernales–Esmeraldas, Km. 50, 3 km N of Río Cojimíes, 00°19′N, 079°55′W, *D. Neill et al. 11699* (MO). **Guayas:** Cord. Chongón-Colonche, 01°48′S, 080°42′W, *C. Bonifaz & C. Cornejo 3544* (MO); Guayaquil–Salinas, Km. 22, summit of Cerro Azul above Casas Viejas, 02°09′S, 079°59′W, *C. H. Dodson & P. M. Dodson 11528* (MO); Teresita, *F. L. Stevens 198* (US); Barraganetal, 02°11′S, 079°18′W, *F. L. Stevens 328* (US); 12 km from Guayaquil, *A. J. Gilmartin 583* (GH, US); Guayaquil–Salinas, Km. 15, Bosque Protector Cerro Blanco, 02°10′S, 079°58′W, *D. Rubio & G. Tipaz 2364* (MO); *T. Núñez & A. Hernández 202* (MO, QCNE); Cerro Azul, Guayaquil–Salinas, Km. 13, 02°10′S, 078°50′W, *G. Tipaz et al. 864* (MO). **Imbabura:** 2 km above Lita along railroad to Imbabura, 00°50′N, 078°28′W, *W. G. D'Arcy 14859* (MO). **Loja:** Loja–La Toma, Km. 12 W of pass, Catamayo valley, 04°00′S, 079°18′W, *B. Øllgaard & P. Lozano 2955* (AAU, QCA); NE slopes of Cerro Mataperro, 3 km SW of San Pedro, 10 km WNW of Catamayo, 03°57′18″S, 079°26′33″W, *F. R. Fosberg & M. A. Giler 22943* (US); Loja–Catamayo, mtns. of Villonaco, 03°59′47″S, 079°18′32″W, *G. Harling 11273* (GB); Cariamanga–Yambaca–El Toldo–Chaco, Km. 10–20, 04°21′S, 079°34′W–04°24′S, 079°31′W, *G. Harling & B. Ståhl 26458* (GB, MO); Vilcabamba–Yangana, 04°18′S, 079°13′W, *G. Harling & L. Andersson 13622* (AAU, GB); Vilcabamba–Yangana, Km. 12–15, 04°20′41″S, 079°11′17″W, *G. Harling & L. Andersson 18480* (AAU, GB); Celica–Alamor, Km. 3, *G. Harling & L. Andersson 22173* (GB); Loja–Catacocha, ca. 25 km S Las Chinches, *G. Harling et al. 15242* (GB); Loja–Catacocha, ca. 10 km S of Las Chinches, 03°59′46″S, 079°31′05″W, *G. Harling et al.15148* (GB); Sozoranga–Reserva Natural El Tundo, Km. 8, fundacion ARCOIRIS, ca. 2–3 km above & past reserve, 04°19′S, 079°49′W, *G. P. Lewis et al. 3499* (E, K, MO); Loja–Catamayo, Km. 7, Villonaco, 03°53′S, 079°19′W, *G. P. Lewis & B. B. Klitgaard 3077* (MO, QCA); San Pedro de Vilcabamba, 04°15′S, 079°15′W, *J. M. MacDougal 1944* (DUKE, MO); Udushi, 03°28′S, 079°24′W, *J. E. Madsen et al. 7412* (AAU, MO, NY); Loja–Portovelo, 03°59′S, 079°12′W–03°43′S, 079°37′W, *J. N. Rose et al. 23343* (GH, NY, US); W of Vilcabamba, 04°17′S, 079°13′W, *J. E. Madsen 36736* (AAU, QCA); Velacruz–Catacocha, Km. 6, 04°00′S, 079°35′W, *E. Øllgaard & Eriksen 90965* (AAU, MO, QCA); El Empalme–Celica, Km. 5, 04°07′S, 079°55′W, *P. M. Jørgensen et al. 55* (GB, MO, NY, QCA, US); San Pedro–Chinchas, *R. Espinosa 1316* (US); *R. Espinosa E1281* (US); Malacatos, *R. Espinosa 1119* (US); La Toma–Catacocha, Km. 21, 03°58′S, 079°30′W, *S. Lægaard 70192* (AAU, QCA); Catamayo–Loja, Km. 7, 03°59′52″S, 079°19′18″W, *S. Knapp & J. Mallet 6261* (BH, CU, QCA, QCNE, US); Celica–Zapotillo, ca. 4 km below Pozul, 03°59′46″S, 079°31′05″W, *G. Harling & L. Andersson 22410* (GB, QCA); Celica–Alamor, via Mercadillo, Km. 8.75, 03°58′S, 080°10′W, *J. F. Smith 1964* (GB, MO, QCA, WIS); El Empalme–Celica, 04°08′S, 079°55′W, *P. M. Jørgensen 65134* (AAU, CU, GB, MO, NY, QCA, U, UPS); Loja, La Argelia, 04°02′01″S, 079°11′50″W, *M. Acosta-Solis 11383* (F). **Los Ríos:** Río Palenque Field Station, Santo Domingo–Quevedo, Km. 47, 00°35′00″S, 079°22′00″W, *A. Gentry 10211* (MO); *C. H. Dodson et al. 7635* (MO); *X. Buitrón & R. Valencia 129* (QCA); Hacienda Clementina, Cerro Samana, La Torre, 01°39′S, 079°20′W, *B. Ståhl & X. Cornejo 5954* (GB); Represa Daule Peripa, Puerto Palmar, 02°10′S, 079°51′W, *C. B. B. 179* (MO). **Manabí:** San Sebastian, Parque Nac. Machalilla, 01°36′S, 080°42′W, *A. Gentry et al. 72606* (MO); Guacharaca–Quimise, 01°30′S, 080°34′W, *C. E. Cerón et al. 16559* (MO); central part of Parque Nac. Machalilla, 01°37′S, 080°40′W, *S. Lægaard 54292* (MO, QCA); Recreo, 00°29′S, 080°27′W, *Eggers 15584* (F, L); Cantón Pedernales, cerro Pata de Pájaro, 10 km E Pedernales, 00°01′N, 079°57′W, *H. Vargas et al. 1239* (MO, QCNE). **Morona-Santiago:** campamento La Playa, 23 km SE of San Juan Bosco, 03°21′S, 078°28′W, *A. Gentry et al. 30934* (MO); El Centro Shuar Kankaim, 02°20′S, 077°41′W, *D. Shiki RBAE261* (NY). **Pichincha:** Dos Rios, Quito–Sto. Domingo, via Chiriboga, Km. 90, *C. H. Dodson & W. R. Thurston 14156* (MO); Km. 96–94, *C. H. Dodson & A. H. Gentry 9714* (MO); Antiguo carr. Quito–San Juan–El Empalme, *A. Freire 533* (QCA); Maquipucuna Reserve, vic. of Nanegal, 6.7 km NE of Nanegalito–Nanegal rd., 00°07′12″N, 078°37′56″W–00°06′42″N, 078°37′49″W, *T. B. Croat et al. 95712* (MO); Quito–Aloag–Sto. Domingo, Km. 94, 10 km S de la carretera, faldas del volcán El Corazón, Hacienda La Esperie, 00°21′S, 078°51′W, *V. Zak 1057* (MO, QCA). **Tungurahua:** *L. K. Albert de Escobar 92-6* (TEX). **Zamora-Chinchipe:** Palanda–Zumba, Km. 6.2, *C. Jiggins 37* (QCA); Km. 28, *C. Jiggins 38* (QCA); N Río Palanda at crossing with Zumba rd., 04°38′S, 079°08′W, *G. Harling & L. Andersson 21284* (AAU, GB, MO, NY, QCA); Zamora, 1 km S of Zamora, 04°04′41″S, 078°57′08″W, *M. T. Madison 2466* (GH). FRENCH GUIANA. 03°38′N, 053°11′W, *L. Skog et al. 7204* (B, CAY, U, US). GUYANA. **Cuyuni-Mazaruni:** Paruima–Konuktipu trail, 05°48′N, 061°03′W, *D. Clarke 1106* (US). **Essequibo Island-West Demerara:** Essequibo, 02°14′N, 059°10′W, *T. Henkel, R. Williams & V. James 2934* (NY, U); 02°15′N, 059°10′W, *A. L. Stoffers et al. 186* (B, MA, NY, U, US). **Potaro-Siparuni:** summit of Ureisha Mtn. above Tipuru, S edge of Pakaraima Mtns., 04°10′N, 059°15′W, *S. Knapp & J. Mallet 2838* (MO). **Upper Takutu-Upper Essequibo:** NW Kanuku Mtns., 12 km ESE Nappi, 03°23′N, 059°29′W, *B. Hoffman 3728a* (U, US). PACIFIC ISLANDS. **Cook Islands:** Kopeka Cave, Pokutelute, *W. A. Whistler 5290* (K). PERU. **Amazonas:** Bagua, camp. El Milagro, just across Río Utcubamba from Bagua Chica, at Km. 228, *S. S. Tillett 672-154* (GH, US); Chachapoyas–Bagua Grande–Olmos, 31 km NE de Olmos, *L. K. Albert de Escobar & P. E. Berry 1526* (TEX); Chachapoyas–Mendoza, Km. 13, *M. Weigend et al. 98/392* (M); Leymebamba–Chachapoyas, *M. Weigend et al. 98/382* (F, M, MO, USM); Balsas–Chachapoyas, Calla-Calla slopes descending from pass, 06°23′37″S, 077°53′41″W, *M. Weigend et al. 98/335* (F, M, MO). **Ayacucho:** Huanta–Río Apurimac, 12°36′25″S, 073°49′58″W–12°35′14″S, 073°49′14″W, *E. P. Killip & A. C. Smith 22800* (F, NY, US). **Cajamarca:** Chirinos–La Palma, Km. 10, 05°25′S, 078°53′W, *A. Gentry et al. 61192* (MO); Monte Seco–El Chorro, Km. 1, Catache, Upper Río Zaña Valley, *M. O. Dillon et al. 4340* (MO); Pacasmayo–Cajamarca, Km. 131, 07°13′S, 078°15′W, *W. D. Stevens 22048* (MO); Contumaza, *A. Sagástegui A. & S. Leiva G. 15531* (F, MO, QCA, TEX); San Benito–Yetón, Andaloy, 07°26′S, 078°56′W, *A. Sagástegui A. et al. 12545* (F, MO); Cascas–Contumazá, *L. K. Albert de Escobar & P. E. Berry 1489* (TEX); Km. 13, 07°25′S, 078°50′W, *B. A. Stein et al. 4023* (MO);

Contumaza–Cascas, 07°24′32″S, 078°47′06″W, *T. E. Boza & G. Rodriguez 2078* (MO); Hualgayoc, Monte Seco, *J. Soukup 3878* (US); Monte Seco, *J. Soukup 3879* (US); Jaén, 3 km al N Santa Rosa, 05°25′09″S, 078°34′12″W, *E. Ortiz & J. Mateo 1208* (AMAZ, HUT, MO, MOL, USM); San Ignacio, La Coipa, Localidad Vista Florida, 05°26′10″S, 078°56′00″W, *J. Campos & Z. García 4042* (MO); San José de Lourdes, Estrella del Oriente, 04°58′00″S, 078°59′05″W, *J. Campos et al. 4813* (MO); 05°00′S, 078°04′W, *R. Vásquez & J. Campos 26184* (MO); arriba de San Francisco, Chaupe, 05°01′08″S, 078°59′32″W, *S. Leiva G. & P. Lezama A. 1614* (F, M, MO, NY, QCA, TEX); Santa Cruz, 06°31′S, 079°04′W, *J. Santisteban C. & J. Guevara B. 140* (F, MO, NY); La Florida above Monteseco, *M. Weigend et al. 7557* (B). **Cusco:** Valle del Río Vilcanota, Amaybamba–Quillabamba, *C. Bues 2129a* (US); Echarate, 12°50′S, 072°39′W, *C. Bues s.n.* (US); Echarate, Piedra Blanca, 12°44′S, 072°33′W, *E. Suclli & J. Farfán 1178* (AMAZ, CUZ, HUT, MO, MOL, USM); Echarate, Sajiruyoc–Belenpata, 12°49′S, 072°34′W, *G. Calatayud 1983* (CUZ, MO, USM); Uchumayo, 12°56′59″S, 072°40′20″W, *F. L. Herrera & Garmendia 2129a* (US); Cusco–Kiteni, ± 150 km NW from Cusco on the rd. from Cusco to Kiteni, 12°49′S, 072°47′W–3°17′S, 072°43′W, *P. Núñez et al. 6804* (MO); Calca, Yanatile, Estrella, 12°26′50″S, 072°30′05″W, *E. Suclli et al. 2439* (CUZ, MO); Lares, Calca, 12°51′44″S, 072°07′36″W, *L. Valenzuela et al. 2701* (CUZ, F, HUT, MO, USM); Distr. Quebrada, Combapata, 12°38′25″S, 072°20′25″W, *L. Valenzuela et al. 1356* (CUZ, MO); La Convención, Echarati, Papelpata, 12°27′S, 072°21′W, *G. Calatayud et al. 2974* (CUZ, MO); Echarate, Kiteni, Agua Dulce, 15°38′33″S, 073°04′07″W, *I. Huamantupa et al. 7205* (CUZ, MO, USM); Maranura, 12°54′47″S, 072°09′54″W, *L. Valenzuela et al. 3118* (CUZ, MO); Santa Ana, Bosque del Chuyapi, 12°56′46″S, 072°46′40″W, *L. Valenzuela et al. 7351* (CUZ, MO); Quillabamba, Salaspampa, 12°49′S, 072°47′W, *P. Núñez & S. Walsh 6368* (MO); 139 km de Cusco en Quellomayo, entre Santa Teresa y Chaullay, 13°08′S, 072°36′W, *P. Núñez V. & F. Motocanchi 8773* (MO); Sahuayaco, Río Chalpimayo, *T. C. Plowman & E. Wade 4871* (GH, K); Huayopata, Cachapampa, 13°11′07″S, 072°37′40″W, *W. L. Galiano et al. 6085* (CUZ, MO, USM); Santa Teresa, 13°11′23″S, 072°36′40″W, *T. E. Boza & P. O. Chambi 2042* (MO); 13°11′38″S, 072°36′43″W, *T. E. Boza & P. O. Chambi 2044* (MO); 13°09′47″S, 072°36′18″W, *T. E. Boza & P. O. Chambi 2045* (MO); 13°09′45″S, 072°36′16″W, *T. E. Boza & P. O. Chambi 2046* (MO); Santa Teresa 13°11′23″S, 072°36′40″W, *T. E. Boza & P. O. Chambi 2048* (MO). **Huánuco:** Huacachi, estacion near Muna, 09°40′15″S, 075°48′41″W, *J. F. Macbride 4162* (F, US); vic. Tingo María, rd. from bridge over Río Chinchao S of Tingo María to Fundo San Juan, *M. E. Mathias & D. Taylor 5319* (F, US); Huánuco, Carpish–Pati, 09°42′S, 076°05′W, *C. Díaz S. & M. S. Baldeón 2255* (MO, QCA); puente Durand, N of Huánuco, valley of Río Chinchao, *H. E. Stork & O. B. Horton 9577* (F, G, NA); Chinchao, 09°38′S, 076°04′W, *J. D. Dwyer 6215* (MO); Tingo Maria–Aguaytía before the Abra Divisoria, Leoncio Prado, 09°12′S, 075°49′W, *K. Weigend et al. 5329* (M, NY). **Junín:** valley of Río Tulumayo, ca. 10 km S of San Ramón, 11°15′S, 075°20′W, *A. Gentry et al. 41532* (MO); Río Colorado, near jct. with Río Chanchamayo, 10°58′S, 075°22′W, *A. Gentry et al. 40137* (MO); Puente Paucartambo to La Merced, Chanchamayo Valley, 11°20′S, 075°20′W, *A. Gentry et al. 39822* (MO); La Merced, 11°02′09″S, 075°19′24″W, *E. P. Killip & A. C. Smith 23400* (F, GH, MA, NY, US); 11°02′09″S, 075°19′24″W, *E. P. Killip & A. C. Smith 23432* (NY, US); 11°03′S, 075°19′W, *J. Schunke 6230* (F, MO); Río Paucartambo Valley, near Perene bridge, 11°02′09″S, 075°19′24″W, *E. P. Killip & A. C. Smith 25371* (US); San Ramón–Oxapampa, 6 km N rd. to Satipo, 10°53′30″S, 075°18′00″W, *T. B. Croat 57723* (MO); Chanchamayo, Cannon of Río Colorado, 10 km N of La Merced, 10°59′S, 075°20′W, *A. Gentry & C. Díaz 73297* (MO); La Merced–Villa Rica, betw. Puente Paucartambo & Río Colorado, 10°54′S, 075°17′W, *D. N. Smith et al. 5614* (MO, TEX); along Río Colorado, N bank W of Puente Colorado, 12 km N of La Merced, *S. Knapp et al. 6344* (BH, CU, US); Junin, Pichis Trail, Yapas, *E. P. Killip & A. C. Smith 25441* (NY, US); San Ramón–Oxapampa, Km. ca. 18–24, *M. O. Dillon & B. L. Turner 1443* (F); Tarma–San Ramón, 11°10′11″S, 075°20′00″W, *G. A. Sullivan et al. 1072* (MO); La Merced–San Ramón, 11°03′S, 075°19′W–11°08′S, 075°20′W, *P. Tovar 4371* (MO). **La Libertad:** Otuzco, arriba de Huaranchal, 07°41′S, 078°27′W, *A. Lopez M. 1341* (MO); Huaranchal, La Libertad, *A. López et al. 2639* (RSA, US). **Lambayeque:** El Lloque, Penachi, *S. Llatas Q. 1451* (F). **Pasco:** La Merced–Oxapampa, 11°03′S, 075°19′W–10°34′S, 075°24′W, *A. Gentry & D. Smith 35785* (MO); Oxapampa, Yanahuanca–Chumalli along Río Pozuzo, 10°31′00″S, 076°29′55″W–10°08′00″S, 076°40′00″W, *D. N. Smith et al. 6322* (MO, US); Oxapampa–Cerro Pajonal–Villa Rica, Km. 12, *M. Weigend & N. Dostert 97/55* (MSB); Oxapampa, Pozuzo–Yanahuanca, along Río Pozuzo, 10°05′00″S, 075°28′00″W, *S. Knapp 6333* (BH, CU, NY, US); Yanahuanca–Chumalli along Río Pozuzo, 10°03′S, 075°25′W, *S. Knapp 6330* (BH, CU, K, US); Río Tres Aguas, Oxapampa–Puente Paucartambi, Km. 34.5, 10°45′S, 075°37′W, *S. Knapp & J. Mallet 6323* (BH, CU, US). **Piura:** Huancabamba, Canchaque–Chorro Blanco, 05°22′S, 079°36′W, *C. Díaz S. & M. S. Baldeón 2451* (F, MO, NY, QCA); Canchaque, Chorro Blanco–War War, 05°22′23″S, 079°36′01″W, *C. Díaz et al. 3197* (MO); below Chorro Blanco, 5 km N of Canchaque, *H. E. Stork 11416* (GH, K, NA); Canchaque–Huancabamba, Km. 11, 05°23′24″S, 079°34′15″W, *M. Weigend & N. Dostert 98/185* (M, MO). **San Martín:** Tarapoto, 06°30′05″S, 076°21′56″W, *E. Ule 6546* (B, G, HBG, L); Chanchamayo, *I. Batilló 2187* (F); San Roque, *L. Williams 7088* (US); Tarapoto–Moyobamba, Km. 72, Lamas, Alonso de Alvarado, San Juán de Pacaizapa, 06°31′58″S, 076°22′09″W, *J. Schunke-V. 9709* (F, G, MO, NY, U); San Martín, *L. Williams 2088* (F). **Tumbes:** Tumbes, mtns. E of Hacienda Chicama, 04°08′13″S, 080°41′43″W, *A. Weberbauer 7653* (F, G, US). VENEZUELA. s. loc. *L. Williams 10121* (F, G, MICH). **Aragua:** Vuelta del Diablo, Vía Choroni, *C. E. Benitez de Rojas 1173* (F, MY, U); El Postachuelo–Ocumare, 10°30′N, 067°46′W, *H. Pittier 11387* (US); Parque Nac. H. Pittier, Maracay–summit of Alto Choroni, 10°21′10″N, 067°35′37″W–10°14′49″N, 067°35′45″W, *T. B. Croat 21459* (MO). **Bolívar:** alrededores de Santa Elena de Uairén, *T. Lasser 1552* (NY); Piar, La Camilera, O del El Manteco, *F. Delascio C. & R. L. Liesner 7050* (MO); Caroni, Cercanias de Lechozal, entre Cd. Guyana y El Pao, 08°07′00″N, 062°43′00″W, *W. Díaz 2538* (MO). **Falcon:** Puente de Jobo, Curimagua–San Luis, *J. A. Steyermark 99246* (NY, US); Parque Nac. Quebrada de la Cueva El Toro, trail going to La Piedra, 10°50′N, 069°07′W, *R. L. Liesner et al. 7813* (MO); 10°50′N, 069°07′W, *R. L. Liesner et al. 7893* (MO). **Miranda:** Chacao, *L. Williams 11191* (F). **Yaracuy:** Buenos Aires–Guamales parte O de la Sierra de Aroa, al N Urachiche, 10°14′N, 069°01′W, *J. A. Steyermark et al. 114090* (MO, NY); Bruzual, Aroa–Cumaragua, 9 km from jct., *L. A. McDade 1027* (DUKE); Bruzual, W of San Felipe, Cocorote–Aroa, mtn. El Cilindro, 10°20′N, 068°49′W, *L. A. McDade et al. 1056* (DUKE, MO).

4. Passiflora citrina J. M. MacDougal, Ann. Missouri Bot. Gard. 76: 354. 1989. TYPE: Honduras. Comayagua: El Carrizal, 14 km NW of Siguatepec, 900 m, 27 June 1971, *A. Molina R. & A. R. Molina 26057* (holotype, F [barcode] 0066761F!; isotypes, EAP!, NY [bc] 00214378!, US [bc] 00588640!). Figures 11, 23D.

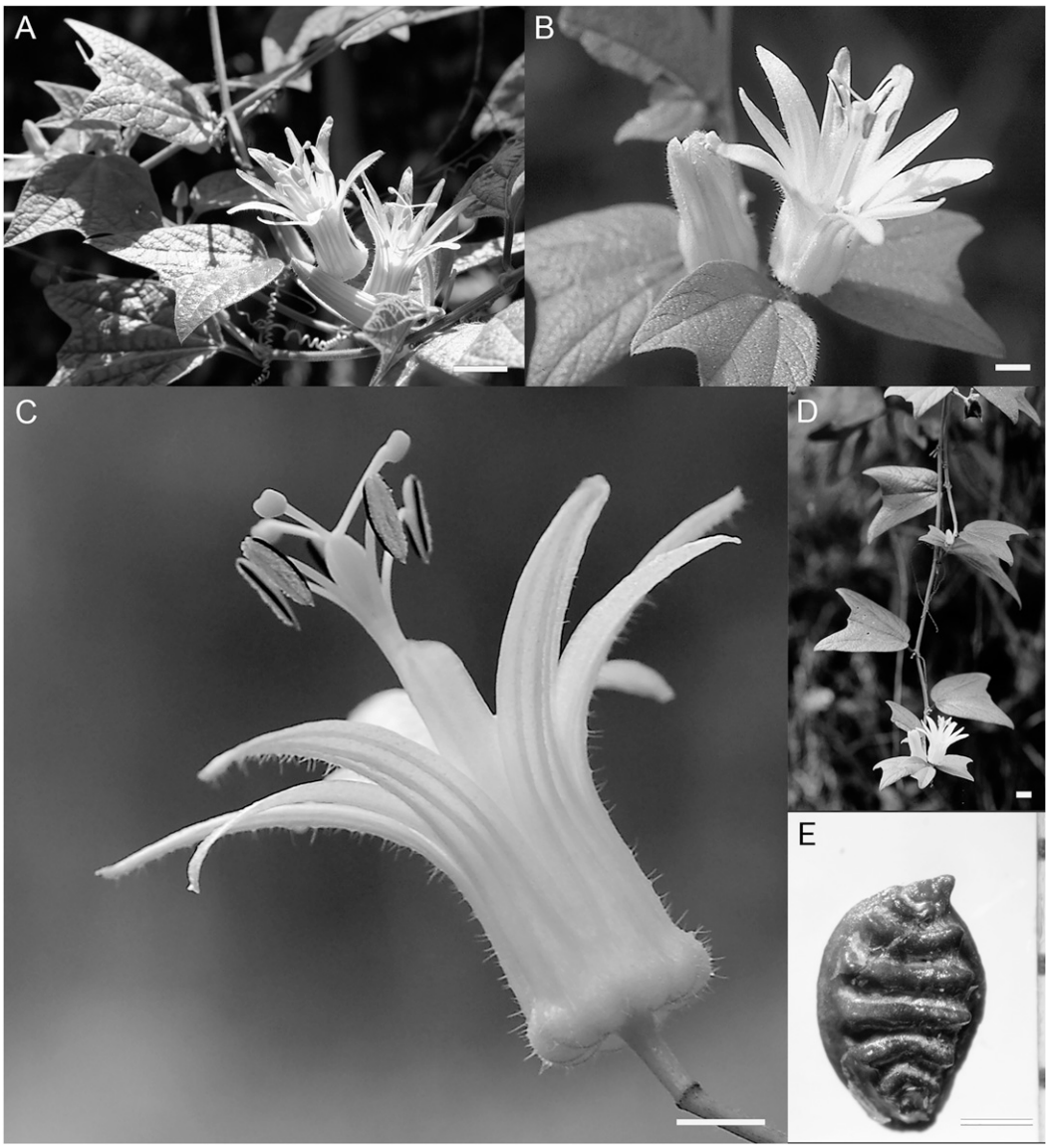

Figure 11. *Passiflora citrina* J. M. MacDougal, all from Honduras or originating from Honduras. —A. Habit showing typical orientation of flowers, cultivated. —B. Flower (*J. M. MacDougal et al. 3469*). —C. Flower, side view, cultivated. —D. Habit (*J. M. MacDougal et al. 3469*). —E. Seed (*A. Molina R. & A. R. Molina 26057*). Scale bars: A, D = 1 cm; B, C = 0.5 cm; E = 1 mm. Photographers: A, Ronald Boender; B, D, John MacDougal; C, Christian Feuillet; E, Tatiana Boza.

Vines 2–4 m, pubescent throughout, with trichomes erect, 0.4–0.8 mm; stems 5-angular, striate; internodes 5.9–8.1 cm. Stipules (2.8–)4.4–5.5(–8.1) × (0.3–)0.6–0.7(–0.8) mm, linear to narrowly triangular, sparsely pubescent abaxially, apex acuminate; petioles (4–)7–10(–19) mm; leaf laminas (2.5–)4.2–5.4(–8.6) × (1.4–)3.3–3.9(–5.8) cm, broadly obovate or obtriangular, rounded or slightly cordate at the base, sparsely pubescent abaxially with trichomes 0.6–0.8 mm, densely pubescent adaxially with trichomes 0.7–0.8 mm, 2(3)-lobed, the lateral lobes acuminate to rounded (when present the small central lobe obtuse to mucronulate); angle between the lateral veins (26°–)43°–48°(–66°). Peduncles (7–)11–13(–24) mm, solitary, exceptionally in pairs, very rarely with 1 bract near the apex; floral stipe 1.3–6.5 mm, to 3.8–7 mm in fruit. Flowers light to bright yellow, floral tube (5.1–)7.6–8.8(–14) × (4.7–)6.2–0.8.4(–12.5) mm; sepals (11.5–)18.4–19.5(–27.4) × (1.8–)2.7–3.3(–5.1) mm, oblong-triangular, sparsely pubescent outside, apex obtuse, light to bright yellow;

petals (9.5–)15.5–16.7(–25.7) × (1.3–)2–2.7(–3.8) mm, narrowly triangular, apex rounded-acute; corona filaments in 1(2) series, pale yellow with yellow tips; filaments of outer series 15, (6.2–)10.7–11.9(–15.5) mm, erect, filiform; when exceptionally present, filaments of inner series (2.2–)4.8–5.8(–8.6) mm; operculum (1–)1.6–1.9(–2.8) mm, slightly plicate; nectary concave; androgynophore (18.9–)20.6–22.2(–28.6) mm; stamens with filaments (3.5–)4.9–5.4(–7.3) mm; anthers (4.1–)5–5.2(–6.2) × (0.9–)1.2–1.5(–2) mm; ovary 3.5–3.8(–5.5) × 1.1–1.5 (–3.2) mm, fusiform to ellipsoid, densely pubescent; styles (2.8–)3.7–4.3(–7) × 0.3(–0.4) mm; stigma 0.6–0.8 (–1.1) mm diam. Fruits (29–)34–38(–42) × (12–) 13–14(–19) mm, fusiform to ellipsoid or slightly ovoid, strongly 6-angular, yellow-green becoming yellow distally or mostly light yellow when mature, rarely tinged with red; seeds (2.7–)3–3.3(–3.6) × (1.6–)1.9–2.1(–2.4) mm, obovate, testa transversely grooved, with 6 or 7 sulci, the ridges continuous, smooth.

Phenology. Flowers of *Passiflora citrina* have been observed in May to December, and fruits have been documented from April to July and from December to January.

Distribution and habitat. *Passiflora citrina* is known from central and western Honduras and adjacent eastern Guatemala and El Salvador (Fig. 5); it has been collected from moist *Pinus* L.–*Liquidambar* L. forest.

Local names. Moco (*Molina & Molina 26821*; Chiquimula, Guatemala).

Discussion. *Passiflora citrina* is characterized by yellow flowers with a distinctive floral tube that is typically 7.6–8.8 mm long, but can be as long as 14 mm. The long tube separates this species from other members of *Passiflora* sect. *Xerogona* except for *P. sanguinolenta*, which can have floral tubes typically 11–14 mm long, or even to 16 mm. *Passiflora sanguinolenta* further differs from *P. citrina* by having triangular stems and pink to red to purplish red flowers that consistently have a second, small row of corona filaments usually only 1.5–1.7 mm long. The second, inner row sometimes seen in some individuals of *P. citrina* is vestigial and very reduced in number. Although section *Xerogona* is characterized by the absence of fertile bracts, *P. citrina* occasionally has been observed with a single bract (1.6–4 × 0.2–0.3 mm) at the apex of the peduncle (*Molina 6510*).

Selected specimens examined. GUATEMALA. **Chiquimula:** La Cumbre on old rd. to Quezaltepeque, 14°37′37″N, 089°23′11″W, *A. Molina R. & A. R. Molina 26821* (EAP, F, U); Olopa, *J. Kufer 379a* (MSB); Volcán Quezaltepeque, 3–4 mi. NE of Quezaltepeque, 14°37′21″N, 089°23′26″W, *J. A. Steyermark 31508* (F). HONDURAS. **Comayagua:** 14 km NW of Singuatepeque, Comayagua, El Carrizal, *Chase 18932* (K); Barranco Trincheras 3 km a Montañuela, 14°39′N, 087°55′W, *A. Molina R. 13637* (EAP, F); Temagua, *J. B. Edwards P-640* (F, GH); NE side of Trincheras just below highest point on Siguatepeque–Lago Yojoa old rd., 14°39′N, 087°55′W, *J. M. MacDougal et al. 3048* (MO); Siguatepeque–Lago Yojoa, Km. 127.5, S side Cerro Trincheras, 14°39′N, 087°56′W, *J. M. MacDougal et al. 3469* (BM, EAP, MEXU, MO, TEFH); Tenagua, Comayagua, *J. B. Edwards 640* (A); San José de Los Planes–Cerro El Maneadero, ca. 13–14 km E of Lago Yojoa, just outside Parque Nac. Azúl Meámbar, 14°47′N, 087°51′W, *R. Evans 1421* (MO); San Juanillo, Cordillera de Montecillos Biological Reserve Forest, 14°30′N, 087°53′W, *R. L. Liesner 26796* (MO); Siguatepeque, bank in ravine 8 mi. W Siguatepeque, 14°34′39″N, 087°54′55″W, *A. Molina R. 31167* (EAP, F, MO); Lake Yojoa–Siguatepeque, Km. 24, 14°38′56″N, 087°55′17″W, *G. E. Pilz & M. Pilz 1572* (MO); Siguatepeque, 10 km N of town on rd. to Lago de Yojoa, 14°39′01″N, 087°56′07″W, *S. Blackmore & M. Chorley 3656* (BM, MO, TEFH); Taulabé, Barranco de Trincheras, 14°39′N, 087°55′W, *A. Molina R. 5826* (EAP, F); Barranco de Trincheras, 18 km N of Siguatepeque, 14°39′N, 087°55′W, *L. O. Williams & A. Molina R. 17991* (EAP, F, US); Trincheras, 20 km N of Siguatepeque, 14°45′N, 087°46′W, *R. A. Howard et al. 637* (B, MICH, NY, US). **Copán:** 5 km SO Santa Rosa de Copán, 14°45′N, 088°49′W, *A. Molina R. 11705* (EAP, F, G, LL, NY, US); *A. Molina R. 11655* (F, NY). **Intibucá:** El Duraznillo, Cordillera Opalaca, 14°13′21″N, 088°14′01″W, *A. Molina R. & A. R. Molina 14086* (EAP, F); La Esperanza, around Balneario, *F. A. Barkley & S. Hernandez 40324* (GH); 14°18′28″N, 088°10′57″W, *J. R. Martinez 110* (BM, MO); *J. Rómulo M. & C. Bejarano 110* (MO); Barranco Yamaranguila, cerca de Yashse [Yase], 14°17′N, 088°16′W, *A. Molina R. 6510* (EAP, F, US); Yamaranguila, La Esperanza–Gracias, Mi. 3.7, Sierra de Opalaca, 14°18′43″N, 088°13′31″W, *G. Davidse et al. 35221* (MO). **Ocotepeque:** La Labor, Nueva Ocotepeque–San Pedro Sula, Km. 41, 14°29′N, 089°03′W, *E. M. Martínez S. & O. Téllez V. 12932* (DUKE, MEXU); Sinuapa, El Moral in Cordillera Merendón, 14°28′N, 089°07′W, *A. Molina R. 22263* (EAP, F, NY); 17 km NE of Nueva Ocotepeque, 14°27′N, 089°07′W, *W. E. Harmon & J. D. Dwyer 3785* (MO).

5. Passiflora cobanensis Killip, J. Wash. Acad. Sci. 14: 111. 1924. TYPE: Guatemala. Chamá to Cobán, 15°36′08″N, 090°36′40″W–15°37′00″N, 090°34′00″W, 26 July 1920, *H. Johnson 411* (holotype, US [barcode] 00036859!, US photo at F [bc] 1083984!). Figures 12, 23E.

Vines 3–6 m, puberulous to densely pubescent throughout; stems 3- to 5-angular, striate. Stipules (6–)7.7–8.6(–10.4) × (2–)2.5–3(–5.1) mm, linear-lanceolate or oblong, ± falcate, sparsely pubescent abaxially; petioles (6–)8–11(–17) mm; leaf laminas (5.6–)7.9–10(–19.6) × (2.6–)3.7–4.5(–7.1) cm, narrowly obovate to very broadly obovate, rounded or slightly cordate at the base, densely hispid abaxially with trichomes 0.1–0.4 mm, sparsely to densely hispid adaxially with trichomes 0.1–0.3 mm, unlobed, strongly 3-nerved in proximal half, angle between lateral veins (18°–)35°–41°(–64°). Peduncles (5–)9–11(–18) mm, usually in pairs; floral stipe 0.8–3 mm, to 1.1–6.6 mm in fruit. Flowers (10–)

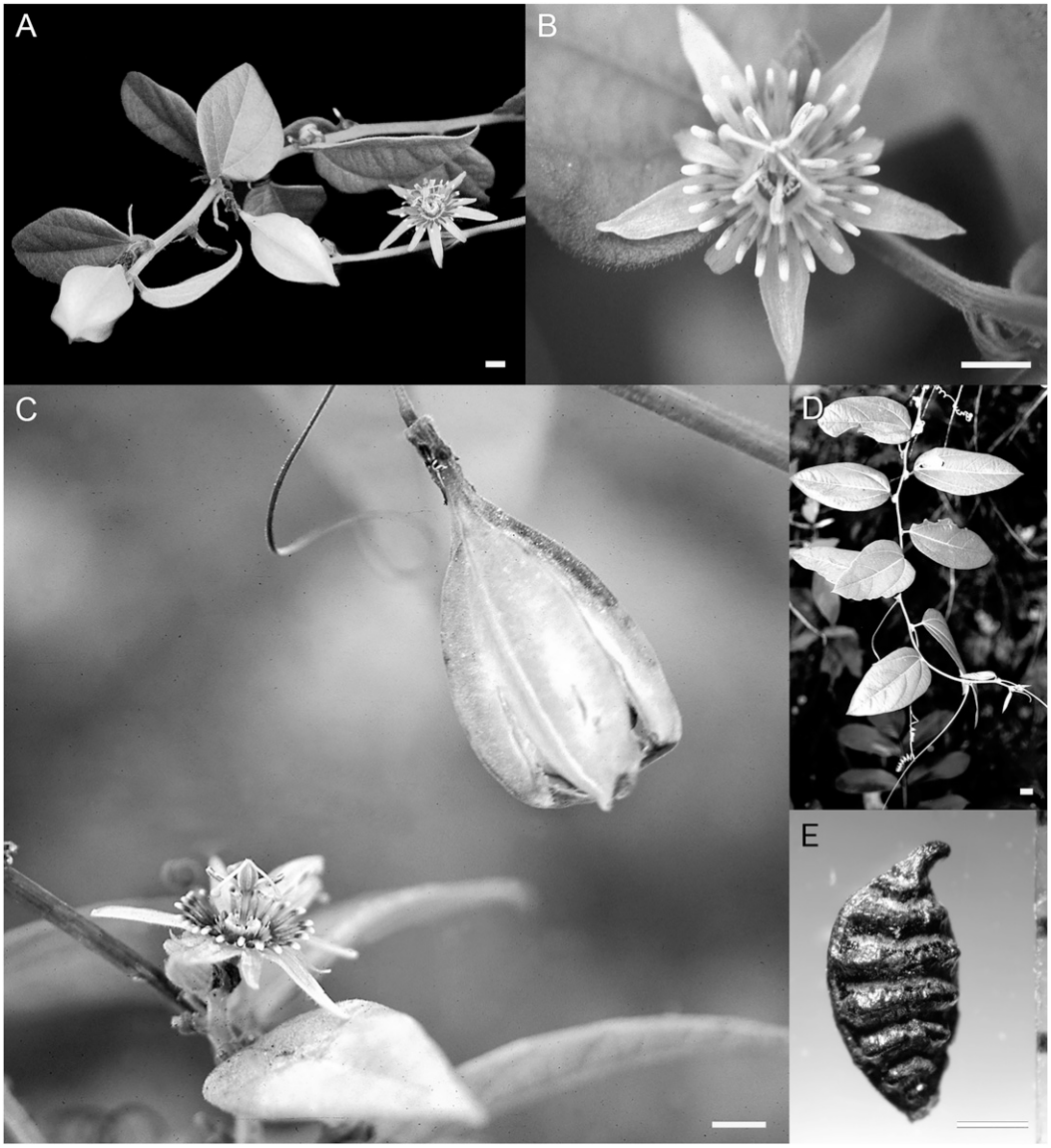

Figure 12. *Passiflora cobanensis* Killip. A–C, E. *Passiflora cobanensis* subsp. *brevipes* (Killip) T. Boza. —A. Leaves, flower, and immature fruit, Galeana, Mexico. —B. Flower, cultivated, origin Belize. —C. Flower and dehiscing fruit, cultivated, origin Belize. —E. Seed, Belize, from the type (*W. Schipp 1304*). D. *Passiflora cobanensis* subsp. *cobanensis*. —D. Habit of pendulous leafy branch, Agua Azul, Chiapas, Mexico. Scale bars: A–C = 0.5 cm; D = 2 cm; E = 1 mm. Photographers: A, León Ibarra González; B, C, Ronald Boender; D, Miguel Molinari; E, Tatiana Boza.

16–20(–29) mm diam., pale green to light greenish yellow; sepals (10.1–)11.8–13(–14.2) × (1.7–)2.4–2.7(–3.4) mm, narrowly triangular, sparsely hirsutulous pubescent outside, apex acute, greenish; petals (4.9–)6.5–6.8(–9.2) × (1–)1.5–1.8(–2.2) mm, linear to narrowly triangular, apex obtuse, greenish; corona filaments in 2 series, exceptionally only 1 series; filaments of outer series 20 to 25, (3–)3.8–4.3(–6) mm, purplish brown and yellowish at the apex, linear-clavate to filiform; filaments of inner series (0.9–)1.4–1.6(–1.8) mm; operculum (1.1–)1.5–1.8(–2.3) mm; androgynophore (3–)3.9–4.1(–5.1) mm, green; stamens with filaments (2.3–)2.9–3.2(–3.8) mm; anthers (1.8–)2.2–2.4(–2.9) × (0.6–)0.9–1.1(–1.2) mm; ovary 1.3–3.5 × 0.7–1.6 mm, obovoid to narrowly obovoid to ellipsoid or slightly fusiform, glabrous to puberulous or densely tomentose; styles (1.7–)2.1–2.5(–3.2) × 0.2–0.3 mm; stigma (0.4–)0.5–0.7(–1.2) mm diam. Fruits (23–)34–38(–49) × (12–)13–16(–24) mm, widely ellipsoid to obovoid,

basally stipitate or attenuate, acutely 6-angled or 6-ridged, reddish brown; seeds (1.9–)3.7–4.1(–5) × (1.6–)2.1–2.3(–2.7) mm, transversely sulcate with 6 or 7 sulci.

Discussion. *Passiflora cobanensis* is unique within *Passiflora* sect. *Xerogona* in having unlobed leaves. It also has conspicuous stipules up to 5 mm wide, unlike the other species of the section which have setaceous to falcate, narrowly linear-triangular stipules. *Passiflora cobanensis* is found from the Atlantic lowland humid forest to lower montane rainforest, especially on ridges and limestone outcrops of Chiapas, Mexico, and extends through central Guatemala to Belize from 120 to 1700 m in altitude (Fig. 7). There are two subspecies within *P. cobanensis*, with one growing in mesic to wet uplands in Chiapas, Mexico, and the second from lowland warmer and seasonally drier areas. MacDougal, in an unpublished manuscript for the *Flora Mesoamericana*, recognized two variants of *P. cobanensis* without formalizing their nomenclature. In the present revision, these variants are recognized as subspecies, based on differences in stem, leaf, corona filaments, ovary characters, and ecological habitat.

Key to the Subspecies of *Passiflora cobanensis*

1a. Stems 4- or 5-angular; stipules oblong, subfalcate; leaf laminas 2.6–5.2 cm wide, thinner, with rounded bases, slightly reticulate beneath and sparsely pubescent; ovaries glabrous or puberulous, only rarely densely tomentose . . . . . 5a. *P. cobanensis* Killip subsp. *cobanensis*

1b. Stems 3-angular; stipules linear to lanceolate; leaf laminas 3–7.1 cm wide, thicker, with cordate bases, conspicuously reticulate beneath with nerves and veins elevated and densely pubescent; ovaries densely tomentose . . . . . 5b. *P. cobanensis* subsp. *brevipes* (Killip) T. Boza

5a. Passiflora cobanensis Killip subsp. **cobanensis.**

Vines 3–6 m, sparsely short hispid throughout; stems 4- or 5-angular, striate. Stipules (6–)7.9–8.6(–10) × (2.2–)2.4–3.1(–4.2) mm, oblong, ± falcate, sparsely pubescent abaxially; petioles (6–)8–12(–17) mm; leaf laminas (7–)9.5–12.8(–19.6) × (2.6–)3.4–4.4(–5.2) cm, margins entire, narrowly obovate, rounded at the base, sparsely to densely hispid abaxially with trichomes 0.1–0.2 mm, glabrous to sparsely hispid adaxially with trichomes ca. 0.1 mm, unlobed, strongly 3-nerved in proximal half and slightly reticulate beneath; angle between lateral veins (18°–)27°–31° (–36°). Peduncles (5–)7–9(–12) mm, usually in pairs; floral stipe 2.4–3 mm, to 3.6–6.6 mm in fruit. Flowers (13–)19–20(–25) mm diam.; sepals (12.2–)12.7–13.9 (–14.2) × (2.9–)3.1–3.3(–3.4) mm, sparsely hirsutulous outside; petals (6–)6.2–7.1(–7.4) × (1.6–)1.8–2.1(–2.2) mm, linear to narrowly triangular; corona filaments in 2 series, rarely 1 series; filaments of outer series ca. 20, (4–)4.1–4.4(–4.5) mm, filiform clavate toward the apex; filaments of inner series (1.1–)1.2–1.5 mm; operculum (1.4–)1.5–1.8(–2) mm; androgynophore (3–)4.3–4.5 mm; stamens with filaments (2.3–)2.9–3.2 mm; anthers (2.2–)2.3–2.6(–2.9) × 0.9–1.1 (–1.2) mm; ovary 1.3–1.6 × 0.7–1 mm, obovoid, glabrous to puberulous, rarely densely tomentose; styles (1.7–)1.8–1.9 mm; stigma (0.4–)0.5–0.7 mm diam. Fruits 44–45(–49) × (12–)18–23(–24) mm, obovoid; seeds (3.8–)4.2–4.8(–5) × (2.2–)2.3–2.4(–2.7) mm.

Phenology. Flowers of *Passiflora cobanensis* subsp. *cobanensis* have been observed in February and fruits have been observed from February to April.

Distribution and habitat. The autonymic subspecies of *Passiflora cobanensis* extends from Chiapas, Mexico, to northern Guatemala. It is found in lower montane rainforests, especially on limestone outcrops or ridges in Chiapas, Mexico, from 300 to 1700 m in altitude.

Discussion. *Passiflora cobanensis* subsp. *cobanensis* and *P. cobanensis* subsp. *brevipes* both grow in Peltalcingo, Chiapas, Mexico, and Alta Verapaz, Guatemala. The subspecies can be distinguished by a stem shape that is 3-angular in subspecies *brevipes*, but 4- or 5-angular in subspecies *cobanensis.* The stipules of *P. cobanensis* subsp. *cobanensis* are oblong and more or less falcate, while those of *P. cobanensis* subsp. *brevipes* are linear to lanceolate. The leaves of subspecies *cobanensis* are longer, narrower, thinner, with a rounded base, acuminate apex, and less indumentum, and are slightly reticulate beneath; in subspecies *brevipes* the leaves are wider, thicker, with a cordate base, acute apex, and dense indumentum, and are conspicuously reticulate with the veins prominent beneath. There are two, rarely one, series of corona filaments in *P. cobanensis* subsp. *cobanensis*, and filaments of the outer series have a clavate apex; in *P. cobanensis* subsp. *brevipes*, the corona always has two series, with the outer filaments filiform and slightly dilated toward the apex. The ovary in subspecies *cobanensis* is obovoid and glabrous to puberulous, whereas in subspecies *brevipes* it is narrowly obovoid to ellipsoid and puberulous to densely tomentose.

Selected specimens examined. MEXICO. **Chiapas:** Ocosingo, Laguna Ocotalito, Monte Líbano–Chancala, Km. 12, 16°57′36″N, 091°35′24″W, *E. Martinez 17075* (MO); *E. Martínez S. 17604* (MO); Palenque–Ocosingo, Km. 70 along the Jol Uk'um, 17°10′12″N, 092°06′36″W, *D. E. Breedlove 50924* (CAS); Agua Azul, 17°15′36″N, 092°06′36″W, *D. E. Breedlove 49862* (CAS, MEXU); Monte Líbano–Hancala, Km. 15, Naha, 16°58′48″N, 091°35′24″W, *E. Martinez 18045* (MEXU, MO); Palenque–Ocosingo, Km. 6–12, 17°27′36″N, 091°57′36″W–17°26′45″N, 091°58′48″W, *D. E. Breedlove 24225* (CAS); Tila, steep slope of Ahk'ulbal Nab above

Peltalcingo, 17°10′41″N, 092°24′20″W, *D. E. Breedlove 49881* (CAS, MO); Tila, Ahk'ulbal Nab above Peltalcingo, 17°10′37″N, 092°24′33″W, *D. E. Breedlove 50409* (CAS, DUKE, MO).

5b. Passiflora cobanensis subsp. **brevipes** (Killip) T. Boza, comb. nov. Basionym: *Passiflora brevipes* Killip, Publ. Carnegie Inst. Wash. 461(13): 312–313, tab. 2. 1936. TYPE: British Honduras [Belize]. Jacinto Hills, 16°15′00″N, 089°00′16″W, 11 Mar. 1934, *W. Schipp 1304* (holotype, F [barcode] 0066760!; isotypes, A not seen, BRH not seen, G [bc] 00191109!, GH not seen, MICH [bc] 1115891!, MICH photo at DUKE!, MO [bc] 193221!, US [bc] 00114972!).

Vines densely short hispid throughout; stems 3-angular, striate. Stipules (6.8–)7.7–8.8(–10.4) × (2–)2.8–3.2(–5.1) mm, linear to lanceolate, sparsely pubescent abaxially; petiole (6–)8–10(–15) mm; leaf laminas (5.6–)6.7–8.2(–11.4) × (3–)3.8–4.6(–7.1) cm, broadly obovate, cordate at the base, densely pubescent abaxially, trichomes 0.2–0.4 mm, glabrous to densely pubescent adaxially with trichomes ca. 0.3 mm, unlobed, strongly 3-nerved in proximal half with conspicuous reticulation beneath (nerves and veins elevated); angle between lateral veins (32°–)42°–50°(–64°). Peduncles (6–)9–11(–18) mm, in pairs; floral stipes 0.8–2.8 mm, to 1.1–5.1 mm in fruit. Flowers (10–)18–23(–29) mm diam.; sepals (10.1–)11.3–12.7(–13.4) × (1.7–)2.1–2.4(–3.3) mm, sparsely hirsutulous pubescent outside; petals (4.9–)6.4–7.3(–9.2) × (1–)1.4–1.6(–2) mm, linear to narrowly triangular; corona filaments in 2 series; filaments of outer series 20 to 25, (3–)3.6–4.2(–6) mm, filiform; filaments of inner series (0.9–)1.1–1.3(–1.5) mm; operculum (1.1–)1.5–1.7(–2.3) mm; androgynophore (3.1–)4.3–4.5(–5.1) mm; stamens with filaments 2.9–3.5(–3.8) mm; anthers (1.8–)2.1–2.3(–2.7) × (0.6–)0.9–1.1 mm; ovary 2–3.5 × 0.9–1.6 mm, narrowly obovoid to ellipsoid, puberulous to densely tomentose; styles (1.8–)2.3–2.8(–3.2) mm; stigma (0.4–)0.5–0.7(–1.2) mm diam. Fruits (23–)30–32(–38) × (12–)13–14(–15) mm, widely ellipsoid to obovoid; seeds (3.6–)3.8–3.9(–4.2) × (1.9–)2.1–2.2 mm.

Phenology. Flowers of this subspecies have been observed from February to June; fruits have been observed in March and from June to July.

Distribution and habitat. Passiflora cobanensis subsp. *brevipes* is known from Chiapas, Mexico, to northern Guatemala and Belize; it has been collected in warm and seasonally dry areas, from 150 to 1700 m in altitude.

Selected specimens examined. BELIZE. **Belize:** Gracie Rock, 1.5 mi. S of Mi. 22 on W hwy., 17°23′N, 088°26′W, *T. B. Croat 23843* (MO, US). **Cayo:** N of Bullet Tree Falls, 1.5 mi. S of Pilar archeological site, 17°13′N, 089°09′W, *J. Walker & D. E. Atha 1536*. **Toledo:** S Maya Mtns., Bladen Nature Reserve, Ek Xux Canyon, ca. 2 km airline NE of Ek Xux archeological site, 16°31′05″N, 088°54′54″W, *G. Davidse 36149* (BRH, MO). GUATEMALA. **Alta Verapaz:** Cerro Chinajá, betw. Finca Yalpemech & Chinajá, above source of Río San Diego, 15°55′54″N, 090°05′36″W, *J. A. Steyermark 45674* (F, US). **Petén:** Dos Lagunas, Ixcanrio rd., Km. 9, 17°41′38″N, 089°31′52″W, *E. Contreras 8722* (LL, TEX); Cadenas, on Morales rd., 15°55′46″N, 089°14′06″W, *E. Contreras 6731* (LL, MO); 15°55′46″N, 089°14′06″W, *E. Contreras 6739* (LL, MO); Dos Lagunas, Ixcanrio rd., Km. 28, 17°44′56″N, 089°18′12″W, *E. Contreras 8694* (MO). MEXICO. **Chiapas:** Ocosingo, Palenque–Boca Lacantum en Crucero Corozal, 16°45′36″N, 091°00′00″W, *E. Martínez S. & M. A. Soto A. 18844* (MO).

6. Passiflora conzattiana Killip, J. Wash. Acad. Sci. 17: 425. 1927. TYPE: Mexico. Veracruz: Mirador, 19°13′N, 096°53′W, June 1921, *C. A. Purpus 8804* (holotype, US [barcode] 00036860!, US photo at B [bc] 10 0293110!, US photo at MICH!; isotypes, F [bc] V0066762F!, GH [bc] 00067999!, MO [bc] 193223, 193224 [2]!, NY!, UC [bc] 211918!). Figure 13.

Vines 0.5–7 m, sparsely pubescent to glabrescent; stems 3-angular, slender, turning reddish brown. Stipules (1.6–)3.6–4.4(–5.6) × (0.2–)0.4–0.5(–0.8) mm, linear to linear-triangular, sparsely pubescent abaxially; petioles (7–)13–17(–29) mm; leaf laminas (1.8–)3.2–4(–6.1) × (3.1–)4.3–5.3(–6.9) cm, depressed obovate, cordate at the base, densely hirsute abaxially with trichomes 0.3–1 mm, sparsely hirsute adaxially with trichomes 0.6–1.2 mm, 2(3)-lobed, the lateral lobes acuminate to acute, when evident the central lobe reduced or cusplike, 3-nerved (nerves often terminating in a short mucro); angle between lateral veins (44°–)79°–87°(–122°). Peduncles (8–)17–20(–44) mm, slender, solitary or rarely in pairs; floral stipe 0.8–3.3 mm, to 3.2–4 mm in fruit. Flowers (16–)19–20(–27) mm diam., greenish white to yellowish green; sepals (4.6–)8.4–9.4(–14.1) × (1.6–)2.1–2.7(–3.9) mm, linear to narrowly elliptic, sparsely hirsutulous outside, yellowish green, apex acute, yellowish green; petals (3.2–)5.9–6.7(–9.4) × (1–)1.4–1.8(–2.5) mm, linear to narrowly elliptic, ca. half as long as the sepals or slightly longer, apex slightly praemorse to retuse, greenish white; corona filaments in 1(2) series; filaments of outer series 20 to 23, (2.2–)3.5–4(–6.2) mm, densely spotted with deep purple in the lower 2/3, yellow in the upper 1/3; filaments of inner series shorter than outer series, (0.7–)0.9–1.2(–1.3) mm; operculum (0.7–)1.1–1.3(–1.9) mm, pale purple; androgynophore 2.4–3.3(–4) mm, green; stamens with filaments (1.8–)2.3–2.7(–3.4) mm; anthers (1.6–)2.1–2.2(–2.6) × (0.5–)0.9–1.1(–1.4) mm; ovary (1.2–)1.7–2(–2.7) × (0.8–)1–1.3(–2) mm, ellipsoid to ovoid or fusiform, densely puberulous; styles (1.1–)1.8–2.1(–2.7) × (0.1–)0.2–0.7(–1.8) mm; stigma (0.5–)0.7–0.9(–1.2) mm diam. Fruits (27–)40–51(–63) × (8–)9–12(–15) mm, narrowly ellipsoid to fusiform,

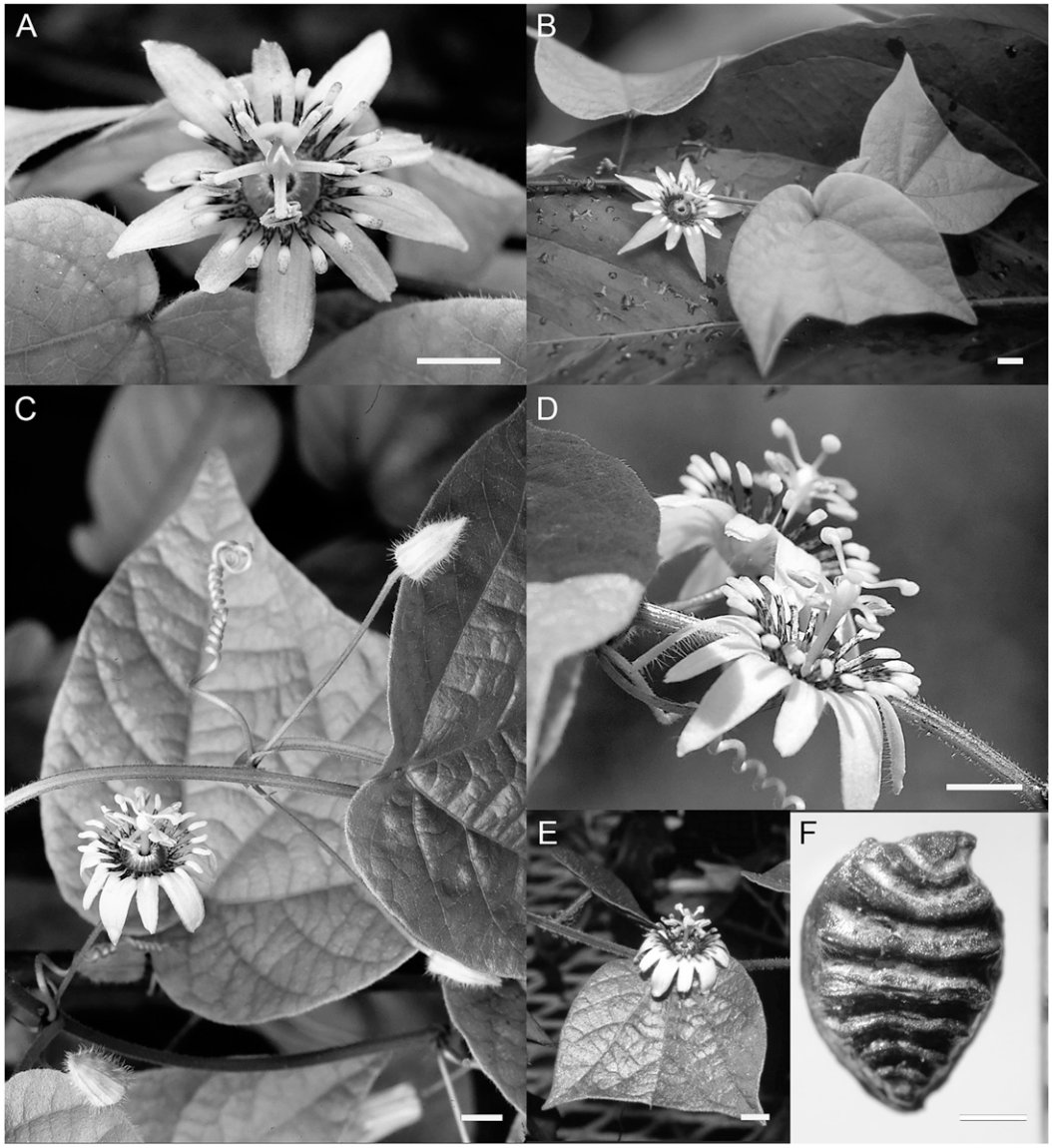

Figure 13. *Passiflora conzattiana* Killip, all material cultivated, except seed. —A. Flower. —B. Flower and leaves. —C. Flower, buds, and leaves, cultivated, origin Veracruz, Mexico (*J. M. MacDougal 548GR*). —D. Flowers, side view. —E. Flower and leaf, cultivated, origin Veracruz, Mexico (*J. M. MacDougal 548GR*). —F. Seed, Veracruz, Mexico (*J. M. MacDougal 3014*). Scale bars: A–E = 0.5 cm; F = 1 mm. Photographers: A, Jorge Ochoa; B, Ronald Boender; C, John MacDougal; D, Marian Oldenbürger; E, Christian Feuillet; F, Tatiana Boza.

finely pubescent to glabrous, 6-keeled, dark purplish red; seeds (2.5–)2.7–3(–3.1) × (1.5–)1.9–2.4(–2.6) mm, transversely sulcate with 5 to 6 sulci, the ridges smooth.

Phenology. Flowers of *Passiflora conzattiana* have been observed from May to August. Fruits have been observed from July to August.

Distribution and habitat. *Passiflora conzattiana* is distributed in east-central Mexico (Fig. 6). The taxon has been collected in wet montane cloud forests from 800 to 1980 m in elevation, principally in wet woodlands of pine and oak forest.

Local names. Ehtitl i okob thut' (*Alcorn 3191*; Huasec, San Luis Potosí, Mexico).

Discussion. The flowers of *Passiflora conzattiana*, *P. cobanensis*, and *P. goniosperma* are quite similar, but the leaf shape and the number of coronal rows in the flower distinguish the species. *Passiflora goniosperma*

has 2-lobed leaves; *P. conzattiana* has 2-lobed leaves, rarely 3-lobed leaves; and *P. cobanensis* has unlobed leaves. *Passiflora conzattiana* has only one, rarely two, series of corona filaments (*Rzedowski 1130*, *Stuessy 838*, *Gonzalez 628*, *Richardson 1351*); *P. goniosperma* has only one series, while *P. cobanensis* has two series of corona filaments.

Although species of *Passiflora* sect. *Xerogona* characteristically lack floral bracts, *P. conzattiana* rarely has a single bract 1.7–2.5 × 0.2–0.4 mm (*Marquez & Dorantes 140A*, *Inzunza 94*).

Selected specimens examined. MEXICO. **Hidalgo:** Tortula [Tortuga], *F. M. Liebmann 4154* (C); Chapulhuacan, 21°09′00″N, 098°54′00″W, *C. L. Lundell & A. A. Lundell 7156* (LL, MICH, TEX, US); 6.5 km air ENE of Jacala, betw. Cuesta Colorado & El Pinalito, 21°01′28″N, 099°08′05″W, *Mayfield 809* (LL, TEX); Molango–Lake Atexca, 20°47′24″N, 098°43′48″W, *H. E. Moore 2992* (BH, CU). **Puebla:** Apulco, Km. 22 de la carr. a Cuetzalán, 20°02′N, 097°32′W, *F. M. Inzunza 94* (CHAPA, F). **Querétaro:** Río Verdito–Agua Zarca, 0.6 km NE of Agua Zarca, 21°13′12″N, 099°06′00″W, *M. Fishbein et al. 5163* (ARIZ); Amoles, aprox. 1 km NE de El Llano, 20°47′N, 100°33′W, *E. Carranza 688* (MO); aprox. 3 km al S de La Tinaja, 21°16′03″N, 099°32′39″W, *E. Carranza 948* (MO); Jalpan, Cerro El Pilón, S de La Parada, 21°26′N, 099°11′W, *C. Guzmán 49* (MO); Landa de Matamoros, ca. 5 km al S de El Parador de El Medroño, 21°12′13″N, 099°19′31″W, *E. González 681* (MO); Puerto del Hambre, ca. 6 km NO de Acatitlán de Saragoza, 21°16′N, 099°09′W, *E. González 628* (MO); Cerca de Neblinas, 21°16′N, 099°05′W, *Rzedowski 46400* (MO). **San Luis Potosí:** Tampico–Canoas, *K. Reiche 669* (M); Ciudad del Maiz, 0.5 km al NE de Las Abritas, 22°29′24″N, 099°23′24″W, *J. Rzedowski 1130* (MICH); Aquismón trail betw. Tampaxal & La Parada, 21°32′N, 099°04′W, *J. B. Alcorn 3191* (DUKE, LL, TEX, XAL); San Luis Potosí, Hills Las Canoas, *C. G. Pringle 3638* (GH). **Tamaulipas:** arriba de Gómez Farias, Rancho del Cielo, 23°03′00″N, 099°12′36″W, *A. Gómez 2040* (GH, MICH); 23°03′N, 099°09′W, *A. T. Richardson 1351* (LL, TEX); 23°03′00″N, 099°12′00″W, *T. Stuessy 838* (LL, TEX); 23°02′24″N, 099°09′00″W, *M. Webster 172* (LL, TEX); Sierra de Guatemala, 23°03′00″N, 099°13′48″W, *J. R. Sullivan 371* (LL, NY, TEX); 23°05′24″N, 099°12′00″W, *J. R. Sullivan 413* (LL, TEX); NE Gómez Farias, rd. to Rancho Cielo, 23°10′N, 099°11′W, 14 July 1972, *Eloy s.n.* (LL, TEX); Tula–Ocampo, Mi. 10.2, 22°56′N, 099°36′W, *G. L. Nesom et al. 6018* (LL). **Veracruz:** El Mirador, 19°13′N, 096°53′W, *C. A. Purpus 16343* (F); 19°13′N, 096°51′W, *H. G. Galeotti 3658* (BR); 19°13′N, 096°51′W, *J. J. Linden 752a* (K); Jalapa, 19°29′N, 096°51′W, *C. G. Pringle 7840* (US); *J. N. Rose & W. Hough 4938* (US); Salto del Gato, E de Xalapa, *Dorantes & Acosta 2011* (ENCB, SLPM); 3 km al O de Xalapa, 19°33′00″N, 096°57′00″W, *Dorantes & Acosta 2069* (ENCB, SLPM); Jalapa, 19°29′51″N, 096°51′47″W, *Rose & R. B. Hough 4260* (US); Altotonga–Tlapacoyan, Atzalan, La Calavera, 19°48′N, 097°13′W, *W. Marquez & J. Dorantes 140* (F, XAL).

7. Passiflora costaricensis Killip, J. Wash. Acad. Sci. 12: 257. 1922. TYPE: Costa Rica. Talamancas: Xirores [Shirores], Feb. 1895, *A. Tonduz 9327* (holotype, US [barcode] 00036862!, US photo at F!, US photo at MO [bc] 940249!; isotypes, BR [bc] 0000694336, 0000694347 [2]!, CR!, US [bc] 00036863!). Figures 14, 23F.

Vines 4–12 m, sparsely to densely tomentose throughout with trichomes 0.5–2 mm; stems sharply 3-angular with angles slightly 3-winged, hirsute with light brown hairs. Stipules (3.1–)6–6.8(–13.5) × (0.6–)0.9–1.1(–1.8) mm, linear to falcate, entire, sparsely pubescent abaxially; petioles (10–)21–28(–64) mm; leaf laminas (7.9–)10.6–12.4(–16) × (5.4–)7.7–8.9(–12.8) cm, broadly obovate, rounded to cordate at the base, densely tomentose abaxially with trichomes 0.5–1.5 mm, densely pilose adaxially with trichomes 0.8–2 mm, 2-lobed, the lateral lobes acuminate or acute, mucronate, 3-nerved; angle between lateral veins (28°–)36°–40°(–59°). Peduncles (6–)9–12(–16) mm, slender, solitary or rarely in pairs; floral stipe 1.9–7.4 mm, to 3.5–11.4 mm in fruit. Flowers (41–)44–46(–52) mm diam., white, cream, or pale greenish white; sepals (13.5–)18.1–19.5(–21.2) × (2.4–)3.9–4.6(–6) mm, linear to triangular, sparsely hirsutulous outside, apex acute, pale green to white, occasionally flushed purple; petals (10.7–)12.6–13.1(–16.4) × (1.9–)3.3–3.8(–5.3) mm, narrowly triangular to narrowly lanceolate, apex obtuse to rounded, white, occasionally flushed purple; corona filaments in 1 or 2 series; filaments of outer series 30 to 36, (8.3–)11–12(–14.8) mm, white or whitish often with a pink or purple base; filaments of inner series shorter than outer series, 1.4–1.6(–1.7) mm; operculum (1.9–)2.2–2.5(–2.9) mm, closely plicate, usually finely pubescent, trichomes ca. 0.6 mm, yellowish green; androgynophore 4.4–7.6 mm, yellowish green; stamens with filaments (2.8–)4.3–5(–6) mm; anthers (2.9–)3.9–4.2(–5.7) × (1–)1.4–1.7(–2.3) mm; ovary 3.1–7.1 × 0.7–3 mm, ellipsoid to fusiform, minutely puberulous; styles (3.5–)4.6–4.9(–6.3) × (0.2–)0.3–0.4(–0.5) mm; stigma (1.1–)1.3–1.5(–2.3) mm diam. Fruits (50–)69–93(–134) × (10–)14–18(–31) mm, ellipsoid or fusiform, rarely obovoid, glabrous, 6-keeled or ridged, dark red to purplish red and often pink to white between the ridges, but nearly all white in Veracruz, Mexico; seeds (1.3–)3.3–3.4(–4.4) × (1.2–)1.8–1.9(–2.2) mm, narrowly ovate, transversely sulcate with 7 to 9 sulci, the ridges smooth.

Phenology. Flowers and fruits of *Passiflora costaricensis* have been observed during most of the year.

Distribution and habitat. *Passiflora costaricensis* is distributed from eastern Mexico to the Pacific coast of Colombia and Ecuador (Fig. 6). The taxon has been collected in lowland to premontane tropical wet forest, from 0 to 1800 m in elevation in the edges of primary forest and in secondary growth.

Discussion. *Passiflora costaricensis* is similar to *P. rubra* but differs by its leaf shape, larger leaves, and

Figure 14. *Passiflora costaricensis* Killip. —A. Habit with leaves and bud, Osa Peninsula, Costa Rica. —B. Side view of flower, Honduras. —C. Flower, buds, and cream-colored dehiscing fruit, cultivated, origin San Andres Tuxtla, Mexico. —D. Immature burgundy-colored fruits, Costa Rica (*J. M. MacDougal 1118*). —E. Cross section of stem, cultivated at RSA (*S. Krosnick 374*). —F. Seed, Ecuador (*C. Quelal & G. Tipaz 340*). Scale bars: A, D = 1 cm; B, C = 0.5 cm; E = 0.1 cm; F = 1 mm. Photographers: A, Reinaldo Aguilar; B, Shirley Sekarajasingham; C, Lawrence E. Gilbert; D, John MacDougal; E, John MacDonald and Shawn Krosnick; F, Tatiana Boza.

thick triangular stem. Its 2-lobed leaves that are longer than broad with a relatively long and conspicuously tomentose indumentum distinguish it readily from *P. rubra*, which has 2-lobed leaves that are broader than long and a hirsute indumentum. Plants at the extreme north of the range in Veracruz, Mexico, have leaves with wider vein angles and a longer indumentum.

Selected specimens examined. BELIZE. **Toledo:** S Maya Mtns., Bladen Nature Reserve, W Snake Creek, 16°27′24″N, 089°01′01″W, *D. L. Holland & B. Kid 95* (BRH, MO). COLOMBIA. Río Mecana, ca. 10 km E of Mecana, 06°15′N, 077°25′W, *A. H. Gentry & A. Juncosa 41089* (COL, JAUM, MO). COSTA RICA. **Alajuela:** Monteverde Reserve, Peñas Blancas river valley, Eladio Cruz farm, 10°20′N, 084°43′W, *W. A. Haber ex E. Bello C. 6171* (MO); Finca de Juan Cruz, 10°18′36″N, 084°03′36″W, *E. Bello 1563* (MO); Reserva Forestal San Ramón, sendero Miramar, 10°12′53″N, 084°36′28″W, *G. Herrera et al. 167* (MO); Alajuela, Reserva Biológica Alberto MI Brenes, 10°13′N, 084°36′W, *J. Homeier 1149* (USJ); San Ramón, N of San Ramón, La Tigra–Fortuna,

Km. 15–35, *C. M. Taylor et al. 4190* (DUKE); Reserva Forestal de San Ramón, 10°13′N, 084°37′W, *J. Gómez-Laurito et al. 12285* (USJ); rd. from San Ramón N through Balsa, ca. 5.7 km N of bridge over Quebrada Volio, 10°07′48″N, 084°28′48″W, *W. D. Stevens 14104* (MO). **Cartago:** Jiménez, Selva, Reserva El Copal, 09°47′00″N, 083°45′20″W, *M. A. Blanco & R. Narit 1874* (USJ); Las Vueltas, Tucurrique, 09°49′48″N, 083°42′36″W, *A. Tonduz 13146* (B, G, US, W); Turrialba, Margen del Río Dantas Parque Nac. Barbilla, 09°58′30″N, 083°27′00″W, *A. Estrada & J. Solano 2558* (K); Parque Nac. Barbilla, Cuenca del Matina, 09°58′20″N, 083°27′10″W, *E. Mora C. 1455* (MO); Terrenos del Instituto, Turrialba, 09°53′24″N, 083°39′00″W, *J. Leon 1696* (US). **Guanacaste:** 26 km from turnoff from Pan-American hwy. to Upala, below Volcan Tenorio, *W. J. Kress 80-1227* (DUKE). **Heredia:** Finca La Selva, the OTS field station on the Río Puerto Viejo just E of its jct. with the Río Sarapiquí, 10°25′53″N, 084°00′13″W, *B. Hammel 11697* (DUKE); Zona Protectora N slopes Volcan Barba, betw. Río Peje & Río Guacimo, along Quebrada Cantarana, *M. H. Grayum & G. E. Schatz 3100* (DUKE); Sarapiquí, Estación Biológica La Selva, *D. Hearn s.n.* (USJ); Zona Protectora, Quebrada Cantarana, Magsasay, 10°22′48″N, 084°03′00″W, *I. A. Chacón 863* (CR, MO); La Selva Biological Station, 10°25′53″N, 084°00′13″W, *J. M. MacDougal 1047* (DUKE); *J. M. MacDougal 1066* (DUKE). **Limón:** Turrialba–Siquirres, Km. 26, *J. M. MacDougal 1118* (CAS, DUKE); Cordillera de Talamanca along Río Madre de Dios, 10°03′00″N, 083°25′48″W, *M. Grayum et al. 8677* (MO); La Colombiana Farm of the United Fruit Co., 10°09′N, 083°35′W, *P. C. Standley 36989* (US); Tsaki, 09°29′24″N, 082°57′36″W, *Tonduz 9594* (BR); betw. La Junta & Florida on the Río Reventazón, 10°06′00″N, 083°33′00″W, *W. W. Rowlee & A. L. Stork 723* (BH, CU, NY, US); Limón, ca. 5 km inland from Limón S to Santa Rosa, *C. J. Taylor 720* (DUKE); Siquirres, Río Barbilla, *J. Gómez-Laurito 4038* (USJ). **Puntarenas:** Parque Nac. Corcovado El Tigre Cerro Mueller, 08°27′N, 083°33′W–08°30′N, 083°38′W, *C. Kernan & P. Phillips 488* (MO); Villa Briceño–Golfito, W side of Fila Gamba, ca. 6 km from Golfito airport, 08°41′24″N, 083°12′00″W, *T. Croat & M. Grayum 59915* (MO); San Vito, Finca Las Cruces, *J. M. MacDougal 210* (DUKE); valley of Laguna Chocuaco, ca. 9 km W of Rincón de Osa, 08°42′00″N, 083°33′36″W, *M. Grayum 4071* (MO); Parque Nac. Corcovado Sirena, 08°27′36″N, 083°34′48″W, *P. Delprete 5130* (LL, MO); Coto Brus, San Vito de Java, Estacion Biológica Las Cruces, 08°47′09″N, 082°57′29″W, *A. Krings 271* (F, USJ); Golfito, Refugio Nac. de Vida Silvestre Golfo Dulce, Peninsula de Osa, Finca de Luis Mata, 08°31′40″N, 083°25′00″W, *A. Azofeifa 485* (MO); Río Tigre, Quebrada Pizote, 08°31′20″N, 083°24′50″W, *A. Azofeifa 792* (USJ); Valle de Coto Colorado, 08°38′50″N, 083°10′05″W, *J. F. Morales et al. 1901* (MO); 08°38′49″N, 083°12′06″W, *J. Gómez-Laurito 13921* (USJ); Estación Agujas, Finca La Leiva de Delfin Vindas, 08°32′22″N, 083°25′07″W, *M. Lobo 203* (MO); La Palma, trocha La Tarde, 08°34′48″N, 083°30′00″W, *R. Aguilar 1748* (CR, MO); Zona Franca (near Golfito)–La Esquina, Km. 6, 08°38′45″N, 083°10′44″W, *W. J. Kress & C. M. Christy 94-4856* (US); Parque Nac. Piedras Blancas, Serranías de Golfito, 08°41′06″N, 083°13′41″W, *L. Acosta et al. 1521* (MO); Osa, no protegida, Cuenca Térraba–Sierpe, 08°49′57″N, 083°16′26″W, *E. Fletes 624* (MO); Los Mogos–Rinco, 08°43′12″N, 083°28′48″W, *G. Herrera 4405* (CR, MO); Parque Nac. Corcovado, 0–1 km from Los Chiles, 08°30′36″N, 083°30′36″W, *R. Liesner 3204* (MO). **San José:** Acosta, Fila Bustamante, Tiquires, 09°43′07″N, 084°12′15″W, *J. F. Morales 4348* (MO). ECUADOR. **Los Ríos:** Centinela–La Pirámide, vía Santo Domingo de los Colorados–Quevedo entrando por Patricia Pilar, Km. 41, 01°40′S, 079°20′W, *C. Quelal & G. Tipaz 340* (MO). **Pichincha:** Patricia Pilar–24 de Mayo, Km. 12, border with Pichincha, ridge line at El Centinela at crest of Montañas de Ila, 00°37′S, 079°18′W, *C. H. Dodson 7292* (AAU, F, MO); vic. of El Centinela, 0.2 km past Escuela Mixta El Centinela, 13 km E of Santo Domingo–Quevedo hwy., 00°32′S, 079°11′W, *T. B. Croat 73012* (MO). GUATEMALA. **Alta Verapaz:** Cubilquitz [Cubilguitz], 15°40′N, 090°25′W, *H. von Türckheim 7877* (GH, US); Chahal airport, 15°46′59″N, 089°35′01″W, *E. Contreras 7956* (LL, MO). **Izabal:** Puerto Barrios, torre de GUATEL, Sierra del Mico, 15°40′18″N, 088°41′33″W, *E. M. Martínez et al. 23587* (MEXU, MO). HONDURAS. **Atlántida:** Tela, Lancetilla valley, above Experiment Station, 15°43′N, 087°27′W, *J. M. MacDougal et al. 3145* (MO); *H. W. Pfeifer 2141* (US); *H. W. Pfeifer 2138* (US); 15°43′00″N, 087°27′30″W, *J. M. MacDougal et al. 3185* (MO); 15°42′40″N, 087°27′28″W, *P. C. Standley 52806* (F, US); 15°44′N, 087°27′W, *T. B. Croat 42591* (EAP, MO); Camp. Quebrada Grande ca. 10 km SW of La Ceiba, N slope of Pico Bonito, 15°42′N, 086°51′W, *R. L. Liesner 26384* (MO). **Cortés:** Lake Yojoa ca. 6 km N of Rancho Agua Azul, *L. O. Williams & A. Molina R. 17776* (EAP, US); Santa Cruz de Yojoa, mtns. E of Lake Yojoa, 14°55′50″N, 088°13′19″W, *C. V. Morton 7760* (F, US). **Yoro:** betw. Río Texíguat & Río Guán, slopes of Cordillera Nombre de Dios in Río León Valley, 15°30′30″N, 087°27′00″W, *J. M. MacDougal et al. 3274* (MEXU, MO, TEFH); mtn. betw. Río Guñan & Río Texíguat S of San Jose in the Río Lean Valley, 15°29′30″N, 087°27′00″W, *J. M. MacDougal et al. 3208* (MEXU, MO, TEFH). MEXICO. **Chiapas:** 7 km SW of Ixtacomitan, 17°25′18″N, 093°08′28″W, *D. E. Breedlove 45938* (CAS). **Oaxaca:** Chinantla, 17°30′00″N, 096°00′00″W, *H. G. Galeotti 3671* (BR, G, P); E of Vistahermosa, ca. 25 km SW of Puente Río Papaloapan at Valle Nac., *W. L. Graham 1405* (MICH); *W. L. Graham 1401* (MICH); Tuxtepec, San Felipe Usila, Nueva Santa Flora, 11 km NNE de San Felipe, 17°54′59″N, 096°26′59″W, *G. Ibarra et al. 3678* (MO). **Veracruz:** 19°12′N, 096°08′W, *G. Ibarra et al. 2979* (MO); San Andres Tuxtla, Estación Biol. Trop. Los Tuxtlas near Catamaco, 18°34′48″N, 095°03′36″W, 13–16 July 1978, *L. Gilber s.n.* (L, LL, TEX); 18°36′N, 095°09′W, *J. B. Fisher et al. 29* (MICH), *J. B. Fisher et al. 40* (MICH); 18°34′48″N, 095°03′36″W, *A. Lot 705* (F, MEXU); *L. Albert de Escobar 1591* (LL); Catamaco, Bastona–Santa Martha, *Gomez-Pompa et al. 5421* (F, XAL); Camino a Balzapote, 1 km N de Estación Biol. Trop. Los Tuxtlas, 18°34′N, 095°04′W–18°36′N, 095°09′W, *S. Sinaca C. & L. M. Mota 878* (MO); Mecayapan, Tatahuicapan–Benigno Mendoza, Km. 7.5, in saddle betw. Volca Santa Marta & Volca San Marti Pajapan, 18°18′00″N, 094°45′36″W, *M. Nee, et al. 25090* (MO). NICARAGUA. **Jinotega:** Wiwilí, Reserva de Bosawas, Tuburus, Uruskirna–Río Bocay, 14°14′N, 085°09′W, *I. Coronado et al. 1080* (MO). **Río San Juan:** El Castillo, 4 km al S de Las Maravillas 11°07′15″N, 084°21′04″W, *R. Guzmán 2256A* (HULE, MO); Boca de Escalera, 4 km al N de Las Maravillas, 11°03′59″N, 084°20′56″W, *R. Guzmán 800A* (HULE, MO). PANAMA. **Bocas del Toro:** hillside above Almirante, 09°18′N, 082°24′W, *A. Gentry 2690* (MO); rd. to Chiriquí Grande, 08°49′36″N, 082°13′06″W, *G. McPherson 7375* (MO); near Chiriqui Grande, on side rd. ca. 10 mi. from continental divide, 08°54′48″N, 082°09′00″W, *G. McPherson 11107* (MO); al N del camp. Changuinola 1 de Corriente Grande, Cerro Bracha, 09°20′42″N, 082°34′24″W, *M. D. Correa A. et al. 3215* (MO, PMA); ca. 15 km S of Changuinola, vic. of Changuinola 1 dam site, 09°18′30″N, 082°32′30″W, *T. M. Antonio 3122* (MO). **Chiriquí:** Burica Peninsula, Quebrada Tuco 15 km S of Puerto Armuelles, 08°07′N, 082°53′W, *R. L. Liesner 168A* (MO).

Coclé: El Copé, Parque Nac. Omar Torrijos, 08°40′06″N, 080°35′34″W, *J. E. Aranda B. & A. Virgo H. 4452B* (F, PMA, US); N slopes of Cerro Caracorral, 08°37′31″N, 080°06′58″W, *J. M. MacDougal 6262* (MO, PMA); trail from Chiguiri toward Cerro Congal, 08°41′26″N, 080°10′42″W, *J. M. MacDougal 6291* (MO, PMA). **Colón:** ca. 2–3 mi. up the Río Guanche, 09°30′30″N, 079°39′30″W, *H. Kennedy & R. Foster 2202* (MO); NW of Mina Boquerón #1, 09°20′N, 079°35′W, *S. Knapp & K. Sytsma 2427* (MO); upstream from bridge over the Río Guanche, 09°30′N, 079°39′W–09°30′N, 079°41′W, *T. M. Antonio 3348* (MO); W of Portobelo, along Río Guanche, E of Colón, 09°30′N, 079°40′W, *G. McPherson 8514* (MO); stream running into Río Buenaventura, S of Portobelo, *R. B. Foster 2061* (DUKE, PMA). **Herrera:** Azuero Peninsula, El Chepo, *A. Aiello & C. Snyder 1467* (PMA); Las Minas, 18 km W of Las Minas, 07°43′04″N, 080°51′54″W–07°43′24″N, 080°51′47″W, *B. Hammel 4310* (MO, PMA). **Los Santos:** Chepo, El Mentuoso, *A. Aiello & C. Snyder 1449* (PMA). **Panamá:** Cerro Campana, trail above FSU Field Station, 08°43′N, 079°54′W, *H. Kennedy et al. 2054* (MO); Sendero al Cerro de la Cruz, 08°40′N, 079°55′W, *M. D. Correa et al. 11345* (PMA); Almirante, Bocas, 11 Nov. 1962, *R. A. Sharp s.n.* (TTC); Capira, Cerro Campana, 08°41′N, 079°55′W, *C. Galdames et al. 1830* (PMA, SCZ). **Veraguas:** above primero brazo del Río Santa Maria, N of Escuela Agicola Alto de Piedra, just W of Santa Fé, 08°34′N, 081°07′W, *S. Knapp & R. Dressler 5380* (MO).

8. Passiflora escobariana J. M. MacDougal, Novon 2: 365, fig. 6. 1992. TYPE: Colombia. Antioquia: Mun. de Frontino, rd. betw. Nutibarra & La Blanquita, region of Murrí, ca. 24.5 km from Nutibarra, 06°40′N, 076°26′W, bosque pluvial premontano, 1090 m, 8 Feb. 1991, *J. M. MacDougal, D. L. Restrepo & D. S. Sylva 3823* (holotype, HUA [barcode] 0000616!; isotypes, BM [bc] 000797797!, COL [bc] 000266275!, CR!, HUA [bc] 0000617!, MEDEL [bc] 000229!, MO [bc] 279964, 279965 [2]!, TEX [bc] 00375734!, US [bc] 00731441!). Figure 15.

Vines 5–10 m, minutely puberulous throughout with trichomes 0.1–0.6 mm, stems 4- to 5-angular, reddish. Stipules (3.6–)4.4–5.2(–6.6) × (0.3–)0.6–0.8(–1) mm, linear-triangular to falcate; petioles (16–)29–36(–61) mm; leaf laminas (7–)8.7–9.9(–11.1) × (7.3–)7.7–8.5(–10.1) cm, broadly obovate, cordate at the base, densely hirsute abaxially with trichomes 0.1–0.3 mm, sparsely hirtellous adaxially with trichomes 0.1–0.6 mm, 2(3)-lobed, the lateral lobes acute to acuminate (when evident the central lobe obtuse); angle between lateral veins (35°–)43°–48°(–58°). Peduncles 14–18(–23) mm, slender, solitary or usually in pairs, red; floral stipe 2.4–4(–8) mm, to ca. 12 mm in fruit. Flowers 40–50 mm diam., cream to whitish or rarely pale pink; sepals (18–)24.1–26.4(–28) × (3–)4–7(–9) mm, narrowly triangular, sparsely hirsutulous outside, apices acute, cream or whitish or less often pale pink at the base; petals (11–)13–16(–17) × 4–5 mm, linear to narrowly triangular, apices acute, whitish to pale pink; corona filaments in 1 or 2 series; filaments of outer series (20 to)24 to 29, (10–)12.4–14.4(–14.5) mm, white in the lower half, pale yellow in the upper half; filaments of inner series 2–2.3 mm; operculum (1.3–)1.6–1.7(–1.9) mm, light purple; androgynophore 7–7.6(–9.7) mm, light greenish; stamens with filaments (4.9–)5.1–5.4(–6.4) mm; anthers (3.6–)4.6–4.7(–5.7) × (1–)1.2–1.3(–1.4) mm; ovary 3.2–5.6 × 1.8–1.9 mm, ellipsoid to fusiform, densely puberulous; styles (4–)4.4–4.8(–5.3) × 0.2–0.4(–0.6) mm; stigma (1.1–)1.4–1.7 mm diam. Fruits 70 × 25–29 mm, fusiform, 6-keeled, red on ridges and cream between; seeds unknown.

Phenology. Flowers and fruits of *Passiflora escobariana* have been observed in February.

Distribution and habitat. *Passiflora escobariana* is distributed from northern Colombia to eastern Panama (Fig. 7). The taxon has been collected in lowland and premontane tropical wet forest, from 100 to 1000 m in elevation at the edge of primary forest.

Discussion. *Passiflora escobariana* is similar to *P. costaricensis* but differs conspicuously by its stems. Its 4- to 5-angular stems distinguish it easily from *P. costaricensis*, which has 3-angular stems.

Selected specimen examined. PANAMA. **Darién:** Parque Nac. Darién, Río Perresénico entre la Estación Pirre y la cascada, 08°00′N, 077°45′W, *H. Herrera 720* (MO).

9. Passiflora goniosperma Killip, J. Wash. Acad. Sci. 17: 424. 1927. TYPE: Mexico. Oaxaca: Mina ["Niña"] de Dolores, Aug. 1842, *F. M. Liebmann 4076*, *Passiflora No. 29* (holotype, C!). Figures 16, 23G.

Vines 3–4 m, hirsutulous throughout; stems sub-3-angular. Stipules (2.4–)3.7–4.1(–6) × (0.3–)0.5–0.7(–1.2) mm, linear, subfalcate, sparsely pubescent abaxially; petioles (2–)7–12(–29) mm; leaf laminas (3.3–)3.8–5.3(–6.9) × (2.8–)3.4–4.8(–7.5) cm, broadly obovate, rounded at the base, densely hirsute abaxially with trichomes ca. 0.3–0.9 mm, densely hirsute adaxially with trichomes ca. 0.8–1 mm, 2-lobed, the lateral lobes obtuse or slightly rounded and often mucronate at the end of the midnerve; angle between lateral veins (31°–)46°–52°(–70°). Peduncles (4–)14–17(–27) mm, usually in pairs or occasionally solitary; floral stipe 1–3.1 mm, to 3–5.5 mm in fruit. Flowers 16–17 mm diam., pale yellow; sepals (6.3–)7.3–7.8(–9.8) × (1.6–)1.9–2.2(–2.8) mm, triangular, sparsely hirsutulous outside, apex acute, pale yellow; petals (3.2–)4.4–5.2(–6.2) × (0.9–)1.3–1.6(–2.3) mm, narrowly elliptic, apices acute, pale yellow with pale purplish red nerves; corona filaments in 1 series; filaments 20, (1.7–)2.2–2.8(–3.3) mm, pale purplish red at the base, pale yellow

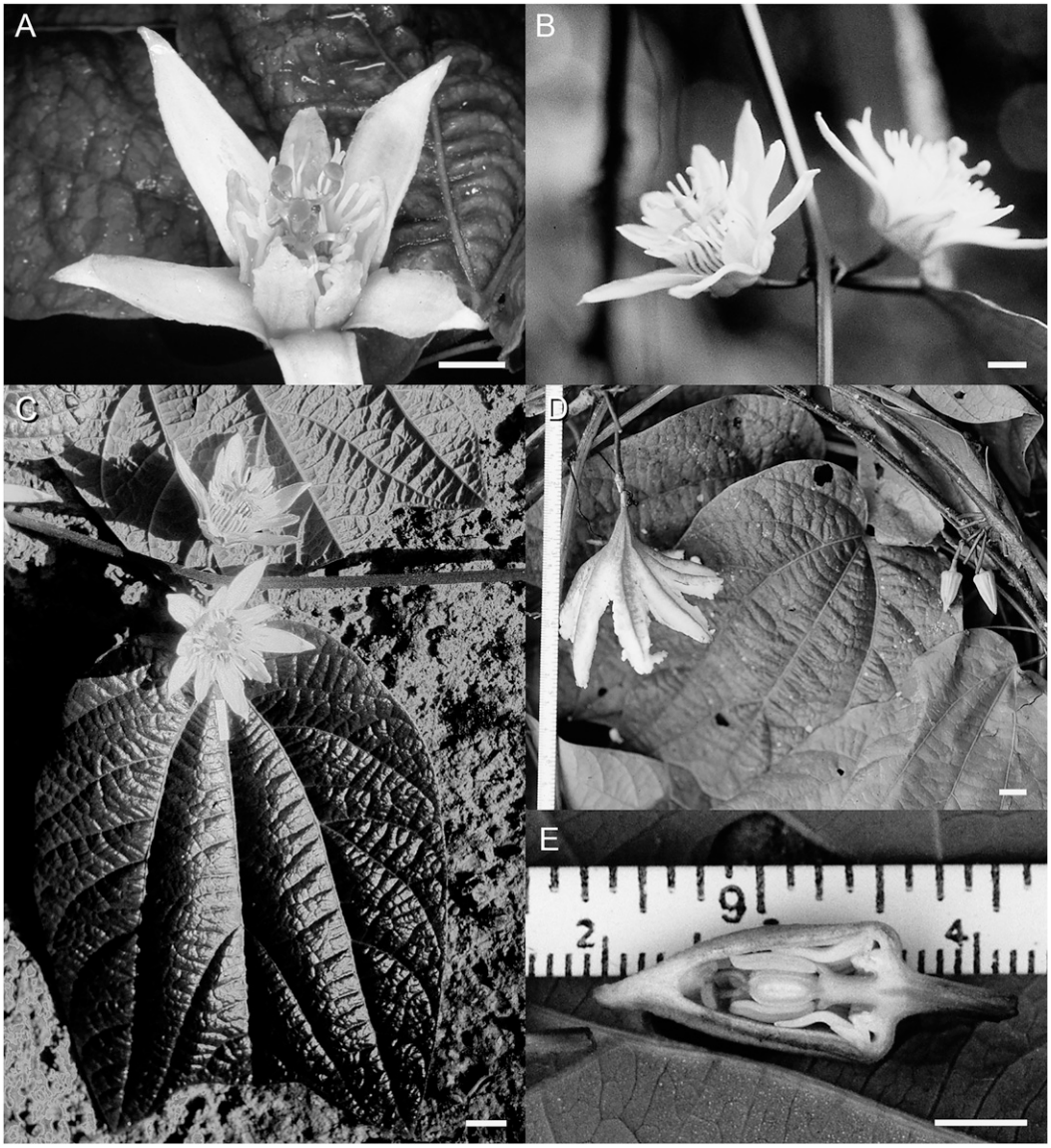

Figure 15. *Passiflora escobariana* J. M. MacDougal. —A. Flower closing in afternoon, cultivated from type material (*J. M. MacDougal 3823GR*). —B. Side view of paired flowers, cultivated (*J. M. MacDougal 3823GR*). —C. Flowers and bullate leaves, cultivated (*J. M. MacDougal 3823GR*). —D. Dehisced fruit, stems, buds, and leaves in field, type collection (*J. M. MacDougal et al. 3823*). —E. Immature bud, longitudinal section in field, type collection (*J. M. MacDougal et al. 3823*). Scale bars: A, B, E = 0.5 cm; C, D = 1 cm. Photographers: A, Lawrence E. Gilbert; B–E, John MacDougal.

or light yellow at the slightly swollen apex; operculum (0.7–)0.9–1(–1.3) mm, closely plicate, pale yellow or pale purplish red; androgynophore 2.7–4.4 mm, green; stamens with filaments (1.6–)2.4–4.1(–4.3) mm; anthers (1.9–)2.3–2.4(–2.9) × (0.6–)1–1.2(–1.3) mm; ovary 1.5–4.1 × 0.7–1.3 mm, ellipsoid or ovoid, yellowish green, puberulous; styles (1–)2–2.2(–3.8) × 0.2–0.3(–0.4) mm; stigma (0.4–)0.5–0.7(–0.9) mm diam. Fruits (31–)36–42(–67) × (7–)8–9(–12) mm, narrowly ellipsoid or fusiform, slightly to sharply hexagonal, 6-keeled, light green or yellowish green at maturity or the ribs flushed with red; seeds (2.9–)3–3.5(–3.7) × (1.7–)1.9–2.1(–2.2) mm, obovoid, strongly compressed laterally, with a narrow longitudinal ridge and transverse grooves reduced to a row of teeth along the longitudinal ridge.

Figure 16. *Passiflora goniosperma* Killip. —A. Flower, cultivated, origin Michoacán, Mexico (*J. M. MacDougal 501GR*). —B. Flower, longitudinal section, Oaxaca, Mexico (*K. E. Porter-Utley 473*). —C. Shoot apex with flower, buds, and leaves; note triangular stem; Oaxaca, Mexico (*K. E. Porter-Utley 473*). —D. Immature fruits, Michoacán, Mexico (*J. M. MacDougal 501*). —E. Seed; note diagnostic toothed ridge in center of face of the testa; Michoacán, Mexico (*J. M. MacDougal 497*). Scale bars: A–C = 0.5 cm; D = 1 cm; E = 1 mm. Photographers: A, D, John MacDougal; B, C, Kristen Porter-Utley; E, Tatiana Boza.

Phenology. Flowers of *Passiflora goniosperma* have been observed from April to August. Fruits have been observed in August and November.

Distribution and habitat. *Passiflora goniosperma* is distributed in southern Mexico (Fig. 7). The taxon has been collected in tropical deciduous forest and dry pine–oak forest from 30 to 1350 m in elevation, mainly in secondary forest edges and roadsides.

Discussion. The seeds of *Passiflora goniosperma* differ from seeds of the other 14 species of *Passiflora* sect. *Xerogona*. These seeds are strongly compressed laterally with a narrow longitudinal ridge. The transverse grooves that normally extend from margin to margin in other species of section *Xerogona* are reduced to a row of teeth along the longitudinal ridge of the seed in *P. goniosperma*. Otherwise, the

dehiscent, narrowly ellipsoid or fusiform 6-keeled fruit and the absence of bracts and foliar nectaries support the relationship of *P. goniosperma* to section *Xerogona*.

Selected specimens examined. MEXICO. **Jalisco:** La Huerta, Rancho Cuixmala, last downhill slope Cumbres 01–Station 45, just before arriving at 45, 19°26′24″N, 104°58′48″W, *E. J. Lott & Phillips 3670* (MO); Cumbres 01, Puerto Vallarta–Barra de Navidad, Km. 45, 19°26′N, 104°59′W, *E. J. Lott et al. 3785* (CAS, LL, MO, RSA, XAL); Arroyo Cajonas, ca. 3 km inland from the Puerto Vallarta–Barra de Navidad hwy., 19°22′48″N, 104°58′48″W, *E. J. Lott et al. 3799* (CAS, LL, MICH, MO, NY); camino antiguo S, Estación de Biol. Chamela (UNAM), 19°30′N, 105°03′W, *E. J. Lott 1741* (DUKE); *E. J. Lott & J. A. Solís M. 1802* (MICH). **Michoacán:** Aguililla, La Placita–Maruata, Mi. 9, 18°26′29″N, 103°32′09″W, *J. M. MacDougal 501* (DUKE, MICH). **Oaxaca:** Santa Gertrudis, *F. M. Liebmann 4075* (C); Sierra San Pedro Nolasco, Talea, 17°22′N, 096°15′W, *Jürgensen 886* (C, FI, MO); Tepanguacales, Sierra de Ixtlán, 17°15′45″N, 096°24′48″W, 1913 [1918?], *Conzatti s.n.* (GH, MO, US); Jamiltepec, al N del Pueblo Dos Caminos, 16°22′43″N, 097°48′15″W, *P. Tenorio L. & R. Torres C. 226* (DUKE).

10. Passiflora pusilla J. M. MacDougal, Ann. Missouri Bot. Gard. 75(1): 392–395. 1988. TYPE: Nicaragua. Chontales: Hacienda Corpus, W of Juigalpa, ca. 100 m, 14 June 1984, *W. D. Stevens 22968* (holotype, MO [barcode] 193217!; isotype, HNMN not seen). Figures 17, 23H.

Herbaceous vines 12–55(–90) cm, hirsutulous throughout; stems triangular or subtriangular. Stipules (0.2–)2–2.7(–4.4) × (0.1–)0.3–0.5(–1.1) mm, linear to linear-triangular, sparsely hirsutulous abaxially; petioles (15–)20–27(–47) mm; leaf laminas (1.2–)2.1–2.7(–4.6) × (2.1–)3.4–4.3(–6.6) cm, depressed obovate, cordate at the base, densely hirsutulous abaxially with trichomes 0.8–1.2 mm, sparsely hirsutulous adaxially with trichomes 1–1.9 mm, 3-lobed, the lateral lobes obtuse or rounded, the central lobe broadly obtuse; angle between lateral veins (79°–)85°–98°(–106°). Peduncles (7–)10–12(–25) mm, solitary; floral stipe 0.8–2.5 mm, to 1.9–3 mm in fruit. Flowers ca. 14.5 mm diam., pale yellowish green; sepals (4.8–)6–6.7(–8.4) × (0.8–)1.2–1.5(–2.2) mm, narrowly triangular, sparsely hirsutulous outside, apex acute, pale yellowish green; petals (3.2–)3.4–4(–4.4) × (1–)1.2–1.5(–2) mm, narrowly elliptic to narrowly ovate, apex acute to rounded, pale yellowish green; corona filaments in 2 series; filaments of outer series 20, (2.1–)3.8–4.3(–5.8) mm, filiform, yellowish green or greenish, yellow toward the apex, with 1 or 2 purplish red bands or mottling near the base; filaments of inner series (1–)1.3–1.4(–1.7) mm; operculum (0.5–)0.8–0.9(–1.1) mm; androgynophore 3–5 mm; stamens with filaments (1.2–)1.5–1.7(–2.1) mm; anthers (1.5–)1.8–2(–2.3) × (0.5–)0.7–0.8(–1) mm; ovary 1.4–2.3 × 0.5–1 mm, narrowly ellipsoid, densely puberulous or tomentose; styles (0.9–)1.8–2.1(–2.8) × 0.1–0.2 mm; stigma 0.3–0.5 mm diam. Fruits 23–30(–50) × 5–8(–10) mm, narrowly fusiform, 6-keeled, sparsely puberulous, green; seeds (2.5–)3.1–3.3(–3.4) × (1.5–)1.7–1.8(–1.9) mm, transversely sulcate with 5 to 6 sulci, with 2 longitudinal rows of 5 to 6 teeth down each margin edge.

Phenology. Flowers of *Passiflora pusilla* have been observed from May to June and from August to December. Fruits have been documented from July to August and from November to December.

Distribution and habitat. *Passiflora pusilla* is distributed in Nicaragua and Costa Rica, with one sterile record from southeastern Mexico (Fig. 5). The taxon has been collected in low tropical moist and dry forests. In Nicaragua and Costa Rica it is associated with the distinctive soil type called *sonsocuite* in Nahuatl, characteristic of poorly drained, seasonally inundated forest (MacDougal, 1988) below 300 m in elevation. *Passiflora pusilla* grows mainly in open areas, roadsides, and pasture edges.

Discussion. *Passiflora pusilla* and *P. tenella* are similar vegetatively, but they have different geographic distributions. *Passiflora pusilla* is distributed in Mexico, Nicaragua, and Costa Rica, while *P. tenella* is endemic to the tropical deciduous forest of Ecuador and Peru. The two species share a much reduced plant size. *Passiflora pusilla* is characterized by having densely pubescent leaves with obtuse or rounded apices on the lateral lobes and a tomentose ovary, while *P. tenella* has less pubescent leaves with acute apices of the lateral lobes and a nearly glabrous ovary. The fruit of *P. pusilla* is hexagonal, while that of *P. tenella* is terete.

Selected specimens examined. COSTA RICA. **Guanacaste:** Parque Nac. Santa Rosa, 30 km W of Liberia, 10°49′48″N, 085°34′48″W, *D. Janzen 12412* (MO); 5 km al NE de Bagaces, 10°33′36″N, 085°16′12″W, *A. Jiménez 2136* (CR, F, NY); 10 km W of Liberia, W of Airport, 10°30′00″N, 085°33′36″W, *R. L. Liesner & R. Lockwood 2516* (MO); 23 km SW of Liberia, 10°24′00″N, 085°33′36″W, *M. F. Tessene 1424* (WIS); Nicoya, Parque Nac. Barra Honda, Península de Nicoya, 10°09′36″N, 085°21′36″W, *M. Reyes et al. 15* (CR, MO). **San José:** Santa Ana, 09°55′48″N, 084°10′48″W, *A. Jiménez 1319* (CR, F). MEXICO. **Oaxaca:** 2 km N of Ixhuatán, *R. Merrill 1983* (LL). NICARAGUA. **Chontales:** Hda. Corpus, W of Juigalpa, 12°07′N, 085°28′W, *W. D. Stevens 22898* (HNMN, MO).

11. Passiflora quinquangularis S. Calderón ex J. M. MacDougal, Novon 14(4): 454–456, fig. 4. 2004. TYPE: El Salvador. San Salvador: S of San Salvador, 13°43′N, 089°12′W, July 1922, *S. Calderón 851* (holotype, US [barcode] 01151809!, US photo at MO [bc] 3605739!; isotypes, GH [bc] 00395044!, US [bc] 01151808!). Figure 18.

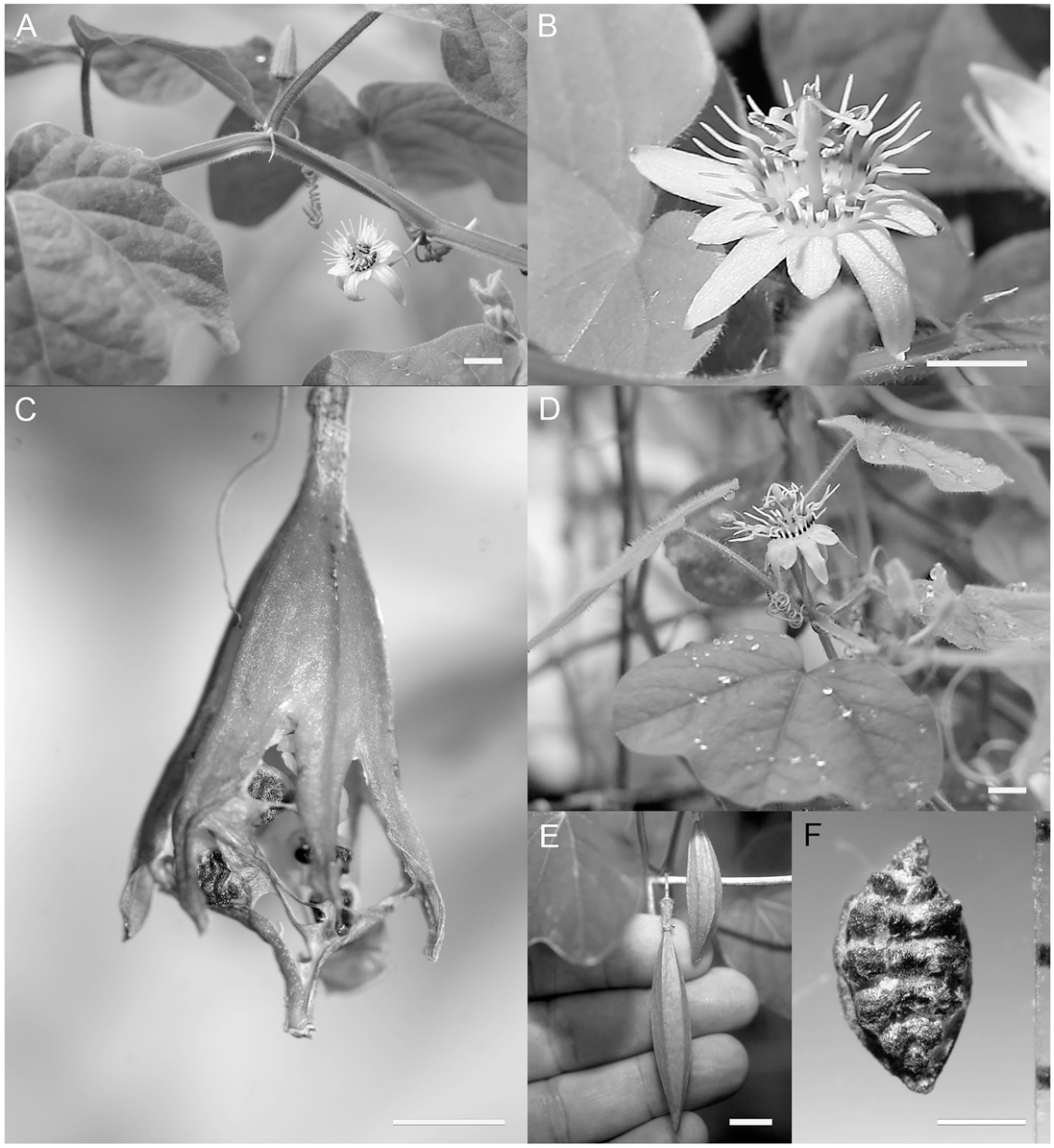

Figure 17. *Passiflora pusilla* J. M. MacDougal, all material originating from Guanacaste, Costa Rica, and cultivated, except seed. —A. Habit; note sharply triangular stem. —B. Flower. —C. Dehiscing fruit, with a low number of seeds produced by autogamy. —D. Habit. —E. Immature fruits, full size but not yet dehiscing. —F. Seed (*A. Jiménez 2136*). Scale bars: A–D = 0.5 cm; E = 1 cm; F = 1 mm. Photographers: A–C, E, Ronald Boender; D, Paula Szilard; F, Tatiana Boza.

Vines 2–4 m, pubescent throughout; stems 5-angular, sometimes glabrescent with age. Stipules (2.2–)3.9–4.6 (–8.4) × (0.3–)0.5–0.7(–1) mm, linear to narrowly triangular, falcate, sparsely pubescent abaxially; petiole (6–)11–14(–24) mm; leaf laminas (4.3–)6.6–8.2 (–12.6) × (3.4–)5.2–6.2(–10.4) cm, broadly obovate, rounded to subcordate at the base, densely hirsute abaxially with trichomes 0.2–0.5 mm, sparsely hirsute adaxially with trichomes 0.4–0.8 mm, 2(3)-lobed, the lateral lobes long, acuminate, when evident the central lobe reduced and cusplike; angle between lateral veins (30°–)41°–50°(–68°). Peduncles (18–)26–36(–90) mm, slender, solitary, rarely in pairs; floral stipe 2.2–4.8 mm, to 5.2–8.5 mm in fruit. Flowers 43–45(–54) mm diam., greenish white to cream; sepals (12.2–)19.6–21.5 (–29.2) × (2.1–)3.8–4.2(–6.4) mm, narrowly triangular, sparsely hirsutulous outside, apex acuminate, light yellow-green and often flushed with red spots abaxially;

Figure 18. *Passiflora quinquangularis* S. Calderón ex J. M. MacDougal, all material cultivated, except seed. —A. Flower, showing typical orientation and slender peduncle. —B. Flower. —C. Leaves and immature fruits. —D. Flower, longitudinal section. —E. Habit, leaves. —F. Seed, El Salvador, from the type (*S. Calderón 851*). A, C, and E, origin Costa Rica (clone from *A. Rodríguez 7550*). B and D, origin Guatemala (*J. M. MacDougal 626*). Scale bars: A, B, D = 0.5 cm; C, E = 1 cm; F = 1 mm. Photographers: A–C, E, Ronald Boender; D, John MacDougal; F, Tatiana Boza.

petals (7.6–)9.8–11.8(–14.8) × (1.1–)1.9–2.4(–3.8) mm, linear to narrowly triangular; apex acuminate or obtuse, white or pale green-yellow; corona filaments in 2 series; filaments of outer series 33 to 39, (5.9–)12.3–14 (–19.5) mm, pure white with purple or purplish red bases; filaments of inner series shorter than outer series, (2–) 2.6–3.3(–4.2) mm; operculum (0.9–)1.6–1.9(–2.4) mm, light purple, white apically; androgynophore 5.8–8.7 mm, green; stamens with filaments ca. 3.5 mm; anthers (3.1–) 3.6–3.8(–4.2) × (0.8–)1.2–1.4(–1.8) mm; ovary 3.1–7.7 × 1.2–3 mm, narrowly ellipsoid or obovoid, densely minutely puberulous; styles (1.9–)3.2–4(–5.4) × 0.2–0.3(–0.4) mm; stigma (0.5–)0.7–1.1(–1.6) mm diam. Fruits 38–49 × 15–16 mm, ellipsoid to broadly fusiform, 6-keeled, slightly puberulous, yellowish green to light yellow apically; seeds (3.1–)3.3–3.6(–3.9) × 1.6–1.7(–1.8) mm, transversely sulcate with 6 to 7 or rarely 8 sulci, ridges smooth.

Phenology. Flowering and fruiting of *Passiflora quinquangularis* have been observed throughout the year.

Distribution and habitat. *Passiflora quinquangularis* is distributed in southern Mexico, Guatemala, and El Salvador, with one record from northwestern Costa Rica (Fig. 6). The taxon has been collected in seasonally dry and deciduous forests from 580 to 1600 m in elevation, principally in thickets and brushy hillsides.

Local names. Bejuco calzoncillo (*González 331*), calzón de mujer (*Chinchilla s.n.*), bejuco calzón de hembra (*González 409*), ala murciélago (*Villacorta et al. RV854*; El Salvador).

Discussion. The name of *Passiflora quinquangularis* refers to the 5-angled stems of this species. *Passiflora quinquangularis* can be confused with *P. rubra*, both having acute or acuminate flower buds, but the buds of *P. quinquangularis* hang down on very slender peduncles, while those of *P. rubra* are more robust and erect. Additionally, *P. rubra* does not occur in Mexico or Central America and is allopatric to *P. quinquangularis*. *Passiflora quinquangularis* can occasionally have a single bract ca. 0.9–1.2 mm long at the apex of the peduncle (e.g., *Cházaro & Leach 3371).*

Selected specimens examined. COSTA RICA. **Guanacaste:** Santa Cruz, Diria, Parque Nac. Diria, cultivada en INBio, 09°58′20″N, 084°05′40″W, *A. Rodriguez 7550* (USJ). EL SALVADOR. **Ahuachapán:** Parque Nac. El Imposible, Las Pilitas, San Benito, 13°49′N, 089°56′W, *A. Sermen 141 (JBL 1056)* (LAGU, MO); 13°49′N, 089°56′W, *E. A. Montalvo & R. Villacorta 6492* (MO); 13°49′N, 089°57′W, *R. Villacorta & S. Martínez 429* (LAGU, MO); 13°49′N, 089°56′W, *Villacorta et al. RV854* (B, LAGU, MO); camino al Mirador del Mulo, 13°49′N, 089°56′W, *R. Morales et al. 1261 (JBL01261)* (CR, MO); Ahuachapán, San Benito al N del pasito, bajadero de los Escobos, 13°49′N, 089°56′W, *E. A. Sandoval 450* (MO); 13°49′N, 089°56′W, *F. Chinchilla s.n.* (B, LAGU, MO); vic. of Ahuachapán, 13°55′17″N, 089°50′42″W, *P. C. Standley 19733* (GH, MO, NY, US); near Concepcion de Ataco, 13°52′13″N, 089°50′55″W, *P. C. Standley & E. Padilla 2644* (F). **La Libertad:** Finca El Paraíso, Jayaque, 13°40′N, 089°26′W, *E. A. Montalvo 4711* (MO); Teotepeque, 13°25′N, 089°31′W, *J. C. González 331* (LAGU, MO); Jayaque, 13°40′N, 089°26′W, *J. González 409* (B, EAP, LAGU, MO). GUATEMALA. **Alta Verapaz:** E of San Pedro Carchá, near Xicacao on rd. to Rubelcruz, 15°29′24″N, 090°04′36″W, *J. M. MacDougal & E. Moroni 6221* (MO). **Baja Verapaz:** O de Salamá, Puente Barranca, 15°06′47″N, 090°18′41″W, *P. Tenorio et al. 14740* (MEXU, MO). **Santa Rosa:** Cuajiniquilapa, 14°16′38″N, 090°17′55″W, *E. T. Heyde & E. Lux 6142A* (GH, US); Santa Rosa, 6 mi. E of rd. to Cuilapa on CA-1, ca. 3 mi. W of intersection of CA-1 & CA-8, *J. M. MacDougal 626* (CU, DUKE, F, MO, US); along rd. SE of Barberena, 14°18′23″N, 090°21′30″W, *P. C. Standley 77729* (F, US); near Cuilapilla, 14°16′47″N, 090°19′20″W, *P. C. Standley 78118* (F). MEXICO. **Oaxaca:** cerca a Santiago Lachiquiri, 16°40′48″N, 095°31′48″W, *M. Cházaro & M. K. Leach 3371* (WIS); Juchitan, 1 km al S de Guevea de Humboldt, 16°47′24″N, 095°21′36″W, *R. Torres et al. 2521* (F, MEXU, MO, XAL).

12. Passiflora rovirosae Killip, J. Wash. Acad. Sci. 12: 259. 1922. TYPE: Mexico. Tabasco, Atasta, 18°00′00″N, 092°57′00″W, 15 June 1890, *J. N. Rovirosa 813* (holotype, PH [barcode] 00014944!, PH photo at F!, PH photo at US!; isotype, K [bc] 000323270 image!). Figures 19, 23I, J.

Vines 4–15 m, puberulous throughout; stems 5-angular, striate. Stipules (3.7–)5–5.8(–8.8) × (0.3–)0.5–0.6(–1.2) mm, linear-triangular, falcate, sparsely pubescent abaxially; petioles (12–)21–26(–35) mm; leaf laminas (5.3–)8.6–9.8(–12.9) × (4.2–)6–6.7(–8.4) cm, narrowly obovate to obovate, deeply cordate at the base, densely tomentose abaxially with trichomes 0.2–0.4 mm, glabrous to sparsely hirsute adaxially with trichomes 0.1–0.6 mm, 2-lobed or truncate at apex, the lateral lobes acute; angle between lateral veins (12°–)21°–26°(–35°). Plants often cauliflorous, the inflorescences being borne on short shoots and thus appearing racemose. Peduncles (5–)10–14(–25) mm, in pairs or rarely solitary; floral stipe 5.2–11.2(–25) mm, to 5.4–18.9 mm in fruit. Flowers (38–)48–54(–64) mm diam., cream or pale yellow; sepals (15.5–)21.7–22.9(–30.4) × (3.5–)4.9–5.6(–7.1) mm, narrowly triangular or narrowly elliptic, apex obtuse, light greenish yellow; petals (11.7–)18.7–19.8(–24.4) × (2.8–)3.5–4.1(–5.1) mm, linear to narrowly triangular with the apex obtuse, cream; corona filaments in 2 series; filaments of outer series 23 to 30, (7.5–)12.8–13.9(–16.5) mm, white or cream tinged with purplish red at the base; filaments of inner series shorter than outer series, (2.1–)2.9–3.4(–5.8) mm; operculum (2–)2.8–3.1(–4.5) mm, closely plicate; limen erect; androgynophore 6.1–10.2 mm, green; stamens with filaments 4.6–4.9 mm; anthers (3.5–)4.7–5(–6.2) × (1–)1.6–1.8(–2.5) mm; ovary 3.1–5.7 × 1.6–2.8 mm, narrowly ovoid, sharply 6-angled, densely puberulous; styles (3.8–)5.2–5.7(–7) × 0.3–0.5 mm; stigma (1.1–)1.6–1.9(–2.8) mm diam. Fruits (65–)72–79(–90) × (18–)24–25(–36) mm, ellipsoid to fusiform, 6-keeled, bright red to dark reddish or purplish red; seeds 3.6–3.8 × 2–2.3 mm, transversely sulcate with 7 to 9 sulci, ridges slightly rugulose.

Phenology. Flowers of *Passiflora rovirosae* have been observed from February to March and from June to December. Fruits have been documented from June to August and from October to December.

Distribution and habitat. *Passiflora rovirosae* is distributed from southeastern Mexico to northeastern Guatemala and Belize (Fig. 7). The taxon has been collected in tropical wet forests from sea level to

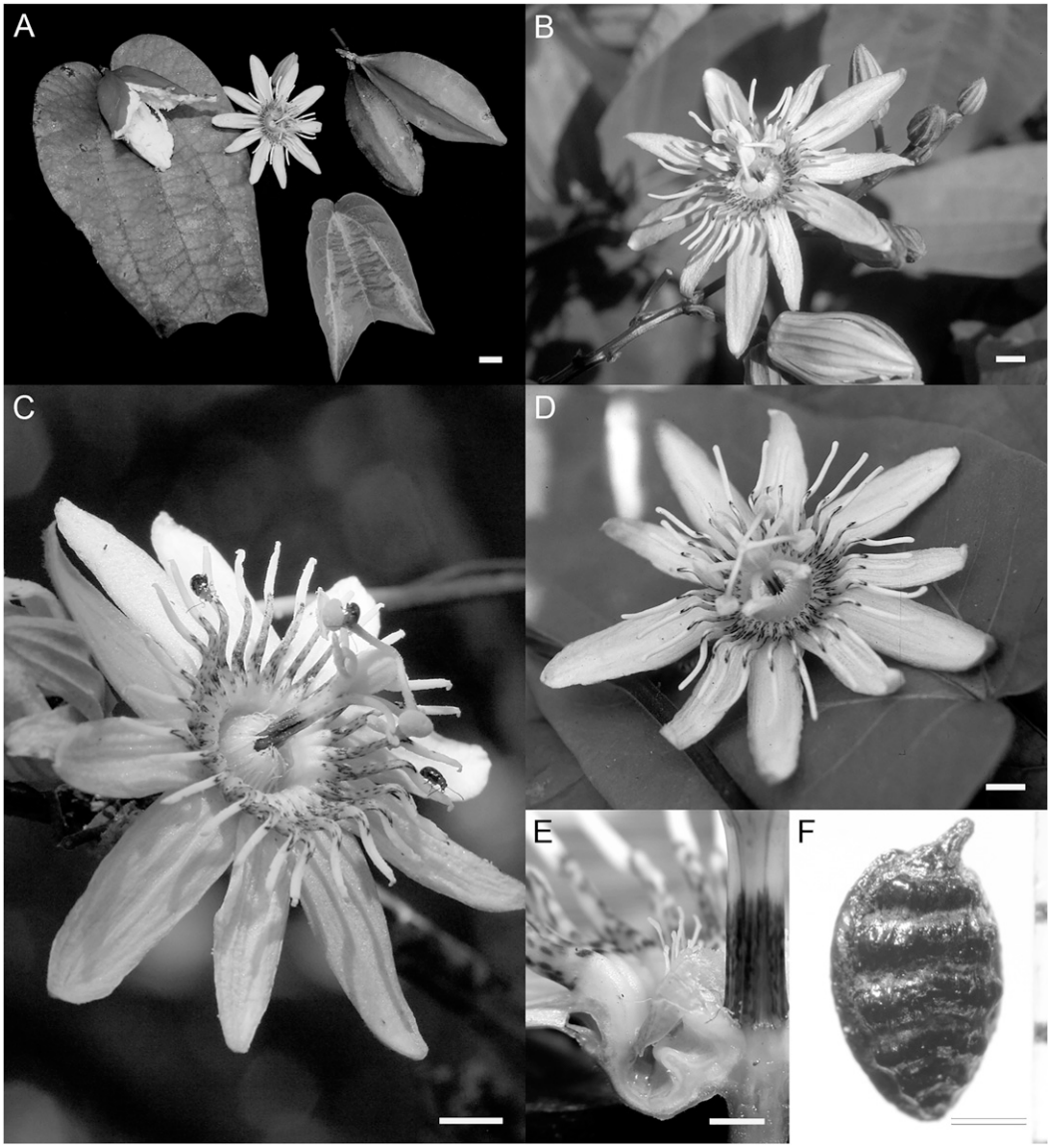

Figure 19. *Passiflora rovirosae* Killip. —A. Arrangement showing dehisced and undehisced mature fruits, flower, and leaves, in Quintana Roo, Mexico. —B. Flower, cultivated, origin Belize. —C. Flower, Puebla, Mexico (*J. Amith 1523*). —D. Flower, cultivated, origin Belize. —E. Flower, longitudinal section showing nectary, operculum, base of corona filaments, and to the right, base of androgynophore; cultivated (*S. Krosnick 377*). —F. Seed, Oaxaca, Mexico (*J. M. MacDougal 2013*). Scale bars: A = 1 cm; B–D = 0.5 cm; E = 0.2 cm; F = 1 mm. Photographers: A, León Ibarra González; B, D, Ronald Boender; C, Jonathan Amith; E, Jorge Ochoa; F, Tatiana Boza.

350 m in elevation, primarily on the edges of primary forest.

Local names. Jujito blanco (*Rovirosa 813*; Atasta, Tabasco, Mexico).

Discussion. *Passiflora rovirosae* and *P. costaricensis* are similar because both have 2-lobed leaf laminas, but *P. rovirosae* can be distinguished from *P. costaricensis* by its short indumentum and 5-angular stem; *P. costaricensis* has a conspicuously 3-angular stem and long indumentum. Very rarely *P. rovirosae* can have a bract-like structure ca. 0.5 mm long associated with the flower (e.g., *Matuda 3283*).

Selected specimens examined. BELIZE. **Corozal:** Cerros Maya Ruins, Lowry's Bight, coastal area, 18°20′58″N, 088°21′51″W, *C. J. Crane 176* (LL); Corozal, 18°23′N,

088°23′W, *P. H. Gentle 434* (US); Paraiso, 18°24′40″N, 088°23′23″W, *P. H. Gentle 810* (A, MICH, MO, US, WIS). **Orange Walk:** Río Bravo Conserv. & Management Area, 17°49′N, 089°02′W, *N. Brokaw & Schulze 195* (MO). **Toledo:** Las Sierritas, 20 km W of Big Creek, S slopes of Cerrito, in the Las Sierritas hills, 16°31′38″N, 088°36′05″W, *T. Hawkins 1678* (MO). GUATEMALA. **Petén:** W des Lago Petén Itzá, Aserradero Covaco, 16°59′08″N, 089°53′00″W–16°59′16″N, 089°54′00″W, *B. Wallnöfer & F. M. Tut-Tesucum 7171* (MO, W); ca. 1.3 km NNE–NE Zentrum von San José, 16°59′26″N, 089°53′00″W–16°59′32″N, 089°54′00″W, *B. Wallnöfer & F. M. Tut-Tesucum 6061* (MO, MSB, W); Uaxactún, 17°23′37″N, 089°38′01″W, *H. H. Bartlett 12691* (CAS, MICH, US). MEXICO. **Chiapas:** Yaxchilán on Río Usumacinta, 16°53′24″N, 090°57′36″W, *D. E. Breedlove 33970* (CAS, DS); Ococingo, Ojo de Agua de San Javier, Crucero Corozal–Palenque, Km. 24, 16°47′24″N, 091°06′00″W, *E. Martínez 15775* (MEXU, MO); Nvo. Guerrero, Palenque–Boca Lacantum, Km. 100, 16°59′24″N, 091°17′24″W, *E. M. Martínez 19080* (MO); Ruinas de Bonampak, 16°55′30″N, 092°07′15″W, *N. Ramírez-Marcial et al. 411* (TEX); Ocozocoautla de Espinosa, cerro El Perico, 17°01′00″N, 093°46′45″W, *ALUSH 9534* (XAL). **Oaxaca:** Tuxtepec, Chiltepec, 17°57′N, 096°11′W, *G. Martinez-Calderon 250* (A, GH). **Tabasco:** San Pedro de Balancan, límite N de la Reserva Federal Sur del Plan Balancan–Tenosique, *J. G. García F. 157* (XAL); La Palma, Balancán, 18°00′36″N, 091°33′43″W, *E. Matuda 3283* (F, MEXU, MICH, US); Teapa, Puyacatengo, 17°31′45″N, 092°55′48″W, *F. Ventura A. 20663* (GH); Tenosique, ca. 15 km arriba de La Palma por el río, a 5 km del Rancho Punta de Montaña del Sr. Angel Zubieta, 17°22′12″N, 091°07′12″W, *C. P. Cowan & Ma. del R. Niño C. 3372* (CAS, MEXU). **Veracruz:** Las Cruces, 17°28′12″N, 093°49′12″W, *Gomez-Pompa & Nevlin 1470* (F); Xinicuila, Sierra Madre Oriental, 8–18 km NW of Campo Experimental de Hule, El Palmar, Zongolica, 18°33′00″N, 096°49′48″W, *J. Vera Santos 3186* (MICH); San Andrés Tuxtla, Estación de Biol. Trop. Los Tuxtlas, cerro Lazaro Cardenas, 18°33′36″N, 095°03′36″W–18°36′00″N, 095°09′00″W, 21 July 1986, *S. Sinaca C. 871* (MO); 13–16 July 1978, *L. E. Gilbert s.n.* (TEX); Hidalgotitlán, Cedillo, *B. Vázquez 1011* (MEXU, XAL); Las Choapas, Rancho El Milagro, 5 km SO de Nueva Tabasquena, 17°31′48″N, 094°01′44″W, *E. López 236* (XAL); Misantla, 19°55′34″N, 096°49′50″W, *C. A. Purpus 5881* (BM, F, GH, MO, UC, US).

13. Passiflora rubra L., Sp. Pl. 2: 956. 1753. *Passiflora verecunda* Salisb., Prodr. Stirp. Chap. Allerton 155. 1796, nom. illeg. superfl. *Granadilla rubra* (L.) Moench, Suppl. Meth. 15. 1802. *Decaloba rubra* (L.) M. Roem., Fam. Nat. Syn. Monogr. 2: 153. 1846. TYPE: tab. 83 in Plumier, Descr. Pl. Amer. 1693 (lectotype, designated by MacDougal et al. [2016: 2]). EPITYPE: West Indies. Windward Islands: Dominica, Carib trail from Salybia to Hatton Garden, promontory overlooking Salybia church, 30 Apr. 1940, *W. H. Hodge 3284* (epitype, designated by MacDougal et al., [2016: 2], NY [barcode] 01921803 image!; isoepitypes, GH!, US [bc] 01193913!). Figures 20, 23K.

Vines 2–3 m, densely, softly pubescent, slightly woody; stems 3- to 4-angular. Stipules (2.7–)4.2–4.9 (–7.1) × (0.2–)0.4–0.6(–0.8) mm, linear to linear-triangular, ± falcate, sparsely pubescent abaxially; petioles (9–)17–23(–40) mm; leaf laminas (4–)5.4–6.6 (–9.5) × (4.7–)7–8.5(–12.4) cm, broadly obovate to depressed obovate, deeply cordate at the base, densely hirsute abaxially with trichomes 0.2–0.7 mm, sparsely hirsute adaxially with trichomes 0.2–0.8 mm, 2-lobed, the lateral lobes acuminate to acute; angle between lateral veins (48°–)66°–75°(–108°). Peduncles (9–)21–25(–62) mm, slender, solitary or in pairs; floral stipe 1–3.5 mm, to 0.8–2.9 mm in fruit. Flowers (27–)35–38(–49) mm diam., greenish white or pale yellow-green, usually suffused with pink; sepals (11.7–)14.8–15.9(–24.5) × (2.2–)3.2–3.8(–5.4) mm, narrowly triangular, sparsely hirsutulous outside, apex slightly acuminate to slightly rounded, pale green to white or rarely pink at the base; petals (6.4–)8.9–9.8 (–11.8) × (1–)1.8–2.1(–2.8) mm, more than 3/4 as long as the sepals (or ca. 1/2 as long), linear to narrowly triangular, apex acute or sometimes slightly praemorse to rounded, white; corona filaments in 1 or 2 series; filaments of outer series 24 to 32, (8.1–)9.9–10.8 (–17.2) mm, intermediate between sepals and petals or as long as the petals, with red, pink, or purplish dots along entire filament length, usually darker toward base, rarely white distally or apically; filaments of inner series, if present, (0.4–)1.3–1.5(–2.3) mm; operculum (1–)1.3–1.5(–2.3) mm; androgynophore 5.5–8 mm, green; stamens with filaments (2.7–)3.8–4.2(–4.8) mm; anthers (2.8–)3.4–3.6(–4.5) × (1–)1.3–1.5(–2) mm; ovary 2.1–4 × 2.1–3 mm, ovoid to subglobose, densely whitish hirsute; styles (1.7–)3–3.5(–4.3) × 0.3–0.4(–0.7) mm; stigma (0.7–)1–1.2 (–1.6) mm diam. Fruits (11–)29–32(–48) × (10–)13–16 (–32) mm, globose to obovoid, hirsute, hexagonal, reddish brown, dark purplish red, or red; seeds (2.7–)3.1–3.4(–3.8) × (1.4–)1.7–1.8(–2.2) mm, transversely sulcate with 6 to 7 sulci, the ridges smooth, with a small projection 0.3–0.5 mm on the chalazal end inclined toward the raphe.

Phenology. Flowers and fruits of *Passiflora rubra* have been observed throughout the year.

Distribution and habitat. *Passiflora rubra* is distributed from the Bahamas, throughout the Greater and Lesser Antilles to Trinidad and Tobago (Fig. 6), at 50–1300 m in elevation.

Local names. Capi twaca, pomme de liane zombie (*Higgins & Paris 98*; Windward Islands); pasionaria de cerca (Killip, 1938; Cuba); liane couleuvre (Killip, 1938; Haiti); bull hoof, Dutchman's laudanum (Killip, 1938; Jamaica).

Discussion. For comments, see *Passiflora capsularis*, *P. cervii*, and *P. cisnana*.

Figure 20. *Passiflora rubra* L. —A. Flower and full-size fruits not yet dehisced, Jamaica or Puerto Rico. —B. Flower, Puerto Plata, Dominican Republic. —C. Flower, St. Lucia. —D. Flower, side view, St. Lucia. —E. Seed, Trinidad (*N. L. Britton & T. E. Hazen 1605*). Scale bars: A–D = 0.5 cm; E = 1 mm. Photographers: A, Elma Kay; B, Henk Wouters; C, D, Roger Graveson; E, Tatiana Boza.

Selected specimens examined. CARIBBEAN ISLANDS. **Bahama Archipelago:** New Providence, near Nassau, 25°05′N, 077°21′W, *A. H. Curtiss 56* (B, BM, BSC, E, F, G, GH, HBG, K, L, M, MIN, MO, NY, P, US); Lake Cunningham, 25°04′N, 077°25′W, *C. F. Millspaugh 2228* (F); 25°04′N, 077°25′W, *E. G. Britton 3301* (F, NY); Village Rd. & Shirley St., Nassau, *D. S. Correll 49304* (NY); S side of Lake Cunningham, 25°01′40″N, 077°25′36″W, *D. S. Correll 50722* (MO, NY); Blue Hill Rd. & Pametto Ave. intersection, Nassau, 25°05′N, 077°21′W, *D. S. Correll 47009* (F, MO, NY); nursery on Fountain Rd., Nassau, 25°05′N, 077°21′W, *D. S. Correll 51385* (DUKE, F, MO, NY); Prospect Waterworks area, 25°04′N, 077°23′W, *G. L. Webster et al. 10491* (DUKE, GH); *L. J. K. Brace 225* (NY); Abaco, *L. J. K. Brace 1758* (NY); *N. L. Britton 133* (NY); E of Clifton Point, 25°01′N, 077°34′W, *O. Degener 18962* (BH, CU, GH, MO, NY, PH); Post [Fort] Charlotte, 25°05′N, 077°23′W, *P. Wilson 8377* (F, NY); Grand Bahama, Sunland Hammock, Freeport, *D. S. Correll et al. 45433* (F, NY); N Andros, Bail rd., 24°42′N 077°46′W, *D. S. Correll 47860* (F, MO, NY). **Barbados:** near Providence, *O. Degener 18931* (GH, NY). **Cuba:** Loma del Palmacito, *B. Eggers 5061* (B, K, US); Cuba Reservoir, *J. T. Bijhouwer 416*

(WAG); in Cuba Orientali, *C. Wright 201* (BR, G, K, MO, NY, PH, S); Oriente, Sierra de Niipe, Farallones de Cayo del Rey, *J. P. Carabia 3534* (NY); La Carmita, Hongolosongo, *B. Clemente 5264* (GH); Saqua el Grande, *E. H. Day s.n.* (NY); Sierra Maestra, inter Río Oro et Río Bayamo, *E. L. Ekman 7263* (RSA, S); Santa Clara, Trinidad Mtns., Buenos Aires, *F. W. Hunnewell 11381* (GH); Trinidad Mtns., summit of Collantes & vic., *R. E. Schultes 184* (GH); hills above Mina Carlota, Trinidad, *T. G. Yuncker 12442* (NY); Yumury, *F. Rugel 351* (B, BM, L, MO, NA, NY, US); San Blas, *L. H. Bailey 12379* (BH); Las Vegas de Mataquá, Buenos Aires, *J. G. Jack 5971* (GH, K, US); Cape Maisi Oriente, 20°15′N, 074°09′W, *L. H. Bailey 15150* (BH, US); El Cuero, *N. L. Britton 12759* (NY); El Junco above Siguanea, in San Juan Mtns., *R. A. Howard et al. 162* (GH, K, MICH, MIN, NO, NY); *R. A. Howard 164* (GH); Camaguey, La Gloria, 21°44′N, 077°39′W, *J. A. Shafer 178* (F, NY); Colonia Limones, Ingenio Soledad, near Cienfuegos, 22°17′N, 080°30′W, *C. G. Pringle 52* (GH); Cieneguita, 22°16′N, 080°37′W, *R. Combs 279* (B, F, GH, MO, NY); Oriente, Holguin, Piedra Gordas, 20°35′53″N, 075°38′14″W, *J. A. Shafer 3492* (B, F, NY, US); Sierra Nipe, near Woodfred, 20°33′29″N, 075°43′09″W, *J. A. Shafer 3054* (NY); La Habana, Loma del Gato, Sierra Maestra, 20°07′00″N, 075°41′00″W, *Bro. Alain 352* (GH); Puerto Boniato, Santiago, *Bro. Alain & Bro. Clemente 825* (GH); Florida Blanca, Alto Songo, *Bro. Clemente 5265* (GH); Jimbambay, Cayo Rey, *Bro. Clemente 2492* (GH); *Bro. Clemente 3098* (GH); Vedado, Habana, Miranda, *F. Leon & Bro. Clemente 20421* (GH); Caval rock hills, Madruga, 22°54′51″N, 081°51′22″W, *J. A. Shafer 465* (NY); vic. of Matanzas, Valley of the San Juan, *N. L. Britton et al. 415* (NY); Pinar del Rio, Reserva de Biosfera de Sierra del Rosario, 22°50′N, 083°00′W, *A. Gentry & O. Valdes L. 71405* (MO); 4–5 km N de Soroa, 22°50′N, 083°02′W, *F. J. Fernández & R. Morales 10769* (CAS, MA, MO, NY); Lomas del Río, Rangel, *León 12535* (NY); Sierra del Rosario, Loma del Salon, 22°45′00″N, 083°10′00″W, *P. Acevedo et al. 005642* (NY); Sancti Spiritus, Loma de Cantú, Banao Mtns., 21°51′N, 079°36′W, *León 5329* (LS, NY); Trinidad Mtns., Siguanea, 21°56′N, 080°00′W, *N. L. Britton & P. Wilson 4905* (NY); Santiago de Cuba, Bayate, 20°22′N, 075°56′W, *E. L. Ekman 1986* (F, S). **Dominican Republic:** banks of Arroyo de Arriba, Sierra de Palo Quemado, Santiago, *A. H. Liogier 10998* (GH); Cabirma de La Loma, San Cristobal, *A. H. Liogier 17762* (NY); Santo Domingo, Jard. Bot. Nac. Rafael M. Moscoso, *A. H. Liogier & P. Liogier 25992* (NY); 18°29′N, 069°57′W, *B. Peguero et al. 1577* (MO); Río Comatillo, Bayaguana, *A. H. Liogier & P. Liogier 21592* (NY); Sierra de Yamasá, Pedregal, loma Los Jobos, 18°39′N, 070°05′W, *B. Peguero et al. 1124* (MO); San Juan, El Cereado, Juan Santiago, Hondo Valle, *R. A. Howard & E. S. Howard 8779* (B, GH, NY, US); vic. of Sanchez, Samaná Peninsula, *W. L. Abbott 178* (US); Layou River Valley, stream NE of Clarke Hall, Brookhill Estate, *E. Wallace 1938* (US); Barahona, *H. von Türckheim 2680* (BR, E, G, GH, HBG, L, M, NY); prope Parubis, *M. Fuertes 443* (B, BM, C, F, G, GH, HBG, K, L, M, MIN, MO, NY, S, US); SE of Polo, *R. A. Howard & E. S. Howard 8426* (GH, NY, US); Enriquillo, 17°54′18″N, 071°14′22″W, *W. L. Abbott 1751* (GH, US); Duarte, Loma Quita Espuela, 19°21′N, 070°09′W, *R. Bastardo et al. 4* (MO); Seibo, Monte Redondo, E of Jovero, *W. L. Abbott 2787* (G, US); 18°59′N, 068°55′W, *W. L. Abbott 2835* (GH, US); La Vega, Los Calabazos across Yaque, 19°04′33″N, 070°43′00″W, *Ososki 172* (NY); 22.4 km S of Jarabocoa, betw. Constanza & Jarabocoa, *R. Carter 5174* (MO); Pedernales–Los Arroyos y Duvergé, Km. 22, Río Mulito, 18°09′N, 071°45′W, 6 May 1982, *T. Zanoni et al. 20405* (MO, NY); carretera al N de Pedernales y al S de Los Arroyos, 18°13′48″N, 071°45′00″W, *W. R. Greuter & R. R. Rodríguez 26623* (B, G, MO, US); loma Pan de Azucar, Samana Peninsula, 12 km NE of Samana, 19°16′N, 069°16′W, *A. Gentry & T. Zanoni 50590* (MO); Sánchez–Las Terrenas, Km. 3, *B. Ståhl & M. Lindstrom 251* (GB); 5 km N of jct. of hwy. Samana & Los Cacaos, on rd. to El Valle, 19°15′N, 069°20′W, *M. Mejía & T. Zanoni 6592* (MO); Las Cañitas, 19°17′N, 069°43′W, *N. Taylor 42* (NY); 3.5 km E Las Terrenas y 4.5 km Sur de la Playa, en Hacienda Nydia, 19°18′00″N, 069°30′30″W, *T. Zanoni & M. Mejía 17788* (NY); San Cristobal en el Pueblo rural de Mano Matuey Arriba, 12.9 km N de Cambita El Cruce, 18°29′00″N, 070°15′00″W, *M. Mejía et al. 19157* (NY); arroyo El Molino, at El Molino, NW base of Loma Siete Picos, due N of Villa Altagracia, 18°44′30″N, 070°11′00″W, *M. Mejía & T. Zanoni 9518* (NY); Santiago, El Choco, Puerto Plata, *F. V. Votava & Alain s.n.* (MO, NY). **Haiti:** Mission, Fonds Varettes, 18°23′27″N, 071°52′11″W, *E. C. Leonard 3668* (NY, PH, US); Dept. du Nord, vic. of St. Michel de l'Atalaye, *E. C. Leonard 7394* (US); vic. of Marmelade, *E. C. Leonard 8319* (NY, US); 19°31′N, 072°21′W, *G. V. Nash 746* (NY); vic. of Furcy, 18°24′43″N, 072°18′20″W, *E. C. Leonard 4767* (BM, F, GH, NY, US); vic. of Mission Varettes, *E. C. Leonard 3685* (US); vic. of Jean Rabel, *E. C. Leonard & G. M. Leonard 13625* (US); La Vallee, Tortue Island, 20°02′N, 072°52′W, *E. C. Leonard & G. M. Leonard 11367* (GH, US), *E. C. Leonard & G. M. Leonard 11549* (NY, US); ridge SE of St. Louis de Nord, 19°54′N, 072°43′W, *E. C. Leonard & G. M. Leonard 14120* (MO, US); vic. of Bombardopolis, *E. C. Leonard & G. M. Leonard 13376* (US); Massif de la Selle, Port-au-Prince, Morne Malanga, *E. L. Ekman 9520* (US); Borgne, *G. V. Nash 418* (NY); 19°50′21″N, 072°31′29″W, *G. V. Nash 562* (NY); San Francisque, *G. S. Miller 287* (US); *Jaeger 138* (B, G, H, US, W); Fondos Verrettes, 18°23′29″N, 071°51′25″W, *L. H. Bailey 183* (BH, US). **Jamaica:** near St. Margarets Bay, 18°11′N, 076°30′W, *A. Fredholm 3272* (NY, US); Lucea, 18°27′N, 078°10′W, *A. S. Hitchcock s.n.* (MO); Porus, 18°02′N, 077°25′W, *F. E. Lloyd 1073* (F, MO); juxta Gordontown, 1882, *J. Ball s.n.* (E); Gordontown to Cinchona, 18°02′00″N, 076°43′00″W–18°04′15″N, 076°40′27″W, *N. L. Britton 50* (NY); Cockpit Country, Banks, Balaclava, 18°10′N, 077°39′W, *N. L. Britton 418* (F, NY, US); Noodstock, *N. L. Britton 1568* (NY); Kingston, 1897, *O. Hansen s.n.* (C); near Troy, 18°15′28″N, 077°35′55″W, *J. R. Perkins 1434* (B, GH); W Clark's Town Trelawny, *U. Hecker 2206* (B); Orange River valley near Montego Bay, 18°27′N, 077°52′W, *W. R. Maxon 1676* (GH, NY, US); Hermitage Dam & vic., 18°04′58″N, 076°46′10″W, *W. R. Maxon 8800* (GH, RSA, US); Ferry River, on the Spanish Town rd., 18°01′N, 076°52′W, *W. R. Maxon 2171* (G, NY, US); Río Cobre, below Bog Walk, 18°06′N, 077°01′W, *W. R. Philipson 598* (MO); vic. of Ewarton, 18°08′57″N, 077°05′22″W, *W. R. Maxon & E. P. Killip 390* (GH); Clarendon, 2 mi. SE of crooked river, *G. R. Proctor 6750* (LL, NY); N slopes of Round Hill, *G. L. Webster & K. I. Miller 8259* (G); Hanover, Hopewell, *L. L. Clarkson & W. J. Kress 75-122* (DUKE); Manchester, Mandeville, 18°02′N, 007°30′W, *Crawford 738* (PH); *G. R. Proctor 22916* (NY); Cockpit Country, ca. 2 mi. SW of Craig Head, *G. L. Webster et al. 8419* (G); Mandeville–Lincoln, 18°02′N, 077°13′W–18°02′N, 077°34′W, *N. L. Britton 3134* (NY); Marshall's Pen, 2.25 mi. due NW of Mandeville, 18°04′00″N, 077°32′53″W, *P. K. Bretting J-126* (MO, NY); St. Andrew, *C. D. Adams 9771* (DUKE); Ferry Pen, Ferry Hill, *G. L. Webster et al. 8075* (G); N slope of Long Mtn., *T. G. Yuncker 17197* (F, G, MICH, NY); St. Ann near Luidas Vale, *F. W. Hunnewell 14347* (NY); near Hopewell, *F. W. Hunnewell 15319* (GH); Reynolds Mine near Lydford P.O., *R. A. Howard & G. R. Proctor 14053* (GH); St. Elizabeth, *I. Maxwell s.n.* (NY); St. Thomas, 1824, *N. Bang s.n.* (C). **Leeward Islands:** Antigua, *H. E. Box 811* (US); hill above

Blubler Valley, 17°03′N, 061°48′W, *J. N. Rose et al. 3459* (B, GH, NY, US); Walling's area, *R. A. Howard 11988* (A, GH); Guadaloupe, Crete de Village, *C. Sastre & F. Sastre 2644* (GH); *A. Questel 5012* (US); *H. Stehlé 1851* (US); *H. Stehlé 2704* (US); Montserrat, slopes of the Centre Hills, above Salem, *G. R. Proctor 18885* (A, GH); St. Kitts, 17°20′N, 062°45′W, *N. L. Britton & J. F. Cowell 103* (NY). **Netherland Antilles:** Saba Mtn., *I. Boldingh 2217B* (U); Rosalie Valley–Morne Jaune Rd., *S. R. Hill 24781* (NY); trailhead of Sandy Cruz Trail from Upper Hell's Gate, 17°38′23″N, 063°14′01″W, *S. A. Mori et al. 25953* (NY). **Puerto Rico:** Adjuntans Rd., 5 mi. from Ponce, *A. A. Heller s.n.* (F, US); the Bucana River E of Ponce, *A. A. Heller s.n.* (NY); SW of Fajardo, *A. H. Liogier et al. 28034* (NY); Río Piedras, 17°50′26″N, 096°45′01″W, *F. Arsene s.n.* (B, NY); ca. 5 km N of Yauco on rte. 128, *C. M. Taylor 7301* (DUKE); N of Peñuelas along rte. 387, ca. 2 mi. from its intersection with rte. 386, *C. M. Taylor 6841* (DUKE); Patillas, along rte. 184, ca. 0.6–0.8 mi. N of the bridge over the Río Grande, *C. M. Taylor 6410* (DUKE); S of Cayey along rte. 15, at Km. 14.7, *C. M. Taylor 6489* (DUKE); Quebradillas, rte. 437, ca. 1–2 km S of rte. 113, 18°25′N, 066°55′W, *C. M. Taylor & R. E. Gereau 10486* (MO); Naguabo, Río Blanco, Caribbean Nat. Forest, 18°12′49″N, 065°44′07″W, *F. Axelrod & P. Chavez 2959* (MO, NY, UPRRP); Juana Diaz, Collores, dirt rd. from end of rte. 512, *F. S. Axelrod & I. Sastre de Jesús 5246* (US); Luquillo, Sabana, Caribbean Nat. Forest, rd. to Río del Cristal, 18°22′28″N, 065°43′01″W, *F. S. Axelrod 5812* (MO, NY, UPRRP, US); Río Piedras, Guaynabo, 18°21′34″N, 066°06′41″W, *F. S. Axelrod & O. Silva 6178* (MO, UPRRP); Toro Negro Forest Reserve, N slope of Monte Jajuya, *F. S. Axelrod et al. 3773* (NY, US); El Río, *G. P. Goll et al. 303* (US); Caguas, *G. P. Goll et al. 374* (US); Candelaria, *G. P. Goll et al. 250* (US); Cerro Ventana, *J. A. Shafer 2987* (NY, US); Fajardo, 18°19′32″N, 065°39′08″W, *N. L. Britton & J. A. Shafer 1698* (NY, US); near Utuado, 18°14′50″N, 066°37′28″W, *N. L. Britton & J. F. Cowell 824* (NY, US); Arecibo, Río Abajo Forest Reserve, 18°19′58″N, 066°43′04″W, *P. Acevedo & B. Angell 9375* (US); Sierra de Luquillo in monte Jimenes, 18°19′N, 065°43′W, *P. Sintenis 1724* (B, MO); Maricao in fruticetis, 18°10′58″N, 066°58′49″W, *P. Sintenis 341* (B, CORD, G, GH, GOET, K, M, MICH, P, S, US); Yauco, 18°02′14″N, 066°51′01″W, *P. A. Garber s.n.* (GH); Sabana rd., N side of Luquillo Mtns., *R. J. Wagner 1245* (GH); Luquillo Mtns., *R. J. Wagner 1756* (GH); Río Piedras, 18°23′58″N, 066°03′01″W, *J. A. Stevenson 153* (MIN, US). **Trinidad & Tobago:** 2 mi. Blanchuesse Rd., 12 Mar. 1960, *H. Fleming s.n.* (NY); Port of Spain, 10°39′N, 061°31′W, *O. Kuntze 786* (NY); Trinidad, Morne Cocoa Rd., *N. L. Britton & T. E. Hazen 1605* (GH, K, NY, US); *F. W. Sieber 241* (B, BM, E, G, L, P, W); Bot. Gard., Lookout hill, 10°39′N, 061°31′W, *W. E. Broadway 6995* (F, K, MO, PH). **Virgin Islands:** St. Croix, Mt. Steward, 3 Jan. 1906, *C. Raunkiaer s.n.* (C); St. Jan Hill, Coral Bay, 2 Mar. 1906, *C. Raunkiaer s.n.* (C); St. John. Francis Bay, 18°21′52″N, 064°44′34″W, *Acevedo et al. 905* (NY, VIST); Reef Bay, Centerline Rd.–Genti Bay, *G. T. Prance et al. 29292* (NY); Maho Bay, intersection of Centerline & Bondeaux Mtn. Rds., *P. Acevedo R. 2438* (NY); Coral Bay Quarter, Bondeaux, 100 m from Centerline Rd., 18°20′14″N, 064°43′17″W, *P. Acevedo & B. Angell 4052* (MO, NY, US); St. Thomas, 18°21′20″N, 064°56′49″W, *B. Eggers 962* (B, BR, G, GH, M, P, US, WU); St. Peter, 17°44′38″N, 064°41′35″W, *E. G. Britton & D. W. Marble 1216* (NY, US); Tortola, shady ghut, Sage Mtn., 18°24′N, 064°39′W, *W. G. D'Arcy 186A* (GH, MO). **Windward Islands:** Dominica, W of High Ridge Rd., Bataka, *J. Higgins & P. Paris 98* (GH, NY); Rosean Valley, 15°30′N, 061°20′W, *E. Lloyd 553* (NY); St. Paul Parish, Sylvania, *D. H. Nicolson 1870* (B, CAS, US); St. Luke, vic. of South Chiltern Estate, 15°15′N, 061°23′W, *W. L. Stern & D. Wasshausen 2526* (B, US); Carib trail from Salybia to Hatton Garden, *W. H. Hodge 3284* (GH, NY, US); Sylvania Estate, *W. H. Hodge s.n.* (GH); Layou River Valley, ridges N of river betw. Layou Village & Cocoa Center, *W. R. Ernst 1987* (GH, US); Martinique, near St. Joseph, *G. Degelius s.n.* (GB); 14°40′N, 061°00′W, *A. Duss 872* (B, NY); Ravine Pilote, 14°40′N, 061°00′W, *L. Hahn 868* (G, K, P); *P. W. Magnus* (HBG); *H. Stehlé 2255* (US); St. Lucia, middle W slope of Gros Piton, *G. R. Proctor 18070* (A); Belfond, 14°N 061°W, *V. Slane 576* (A); St. Vincent, along Chateaubelair, *C. V. Morton 5108* (US); 13°14′25″N, 061°11′08″W, *H. H. Smith & G. W. Smith 607* (B, E, GH, HBG, K, NY).

14. Passiflora sanguinolenta Mast. & Linden, Gard. Chron. 1868: 1162. 1868. TYPE: Peru. *W. Lobb 151* (neotype, designated here, K [barcode] 000323350 image!). Figures 21, 23L.

Passiflora mastersiana Harms, Bot. Jahrb. Syst. 18 (Beibl. 46): 8. 1894. TYPE: Ecuador. Loja, "in silvis apertis circa Las Yuntas [Juntas] et Pucala," 1800–2200 m, *Lehmann 4836* (holotype, B†; lectotype, designated here, K [barcode] 000323351 image!; isolectotype, K [bc] 000323352 image!).

Vines 2–3 m, densely villous throughout; stems 3- to sub-4-angular, striate. Stipules (1.3–)2.8–3.4(–5.9) × (0.2–)0.3–0.4(–0.8) mm, linear, setaceous; petioles (5–)12–17(–44) mm; leaf laminas (2.1–)3.7–4.7(–10.2) × (3.2–)4.4–5.7(–12.2) cm, depressed obovate, cordate at the base, densely hirsute abaxially with trichomes 0.2–0.8 mm, sparsely hirsute adaxially with trichomes 0.2–0.8 mm, 2(3)-lobed, the lateral lobes obtuse to acuminate, when evident the central lobe reduced and obtuse; angle between lateral veins (42°–)56°–64°(–85°). Peduncles (4–)18–21(–40) mm, solitary or rarely 2; floral stipe 2.5–4.8 mm, to 3.9–9.5 mm in fruit. Flowers pink to red to purplish red; floral tubes (9–)11–14(–16) × (4–)6–7(–11) mm, reddish; sepals (19.4–)25–26.5(–29) × (3.2–)3.6–4.8(–5.8) mm, narrowly triangular, sparsely hirsutulous outside, apex acuminate, reddish; petals (15–)17.8–21.5(–24.1) × (1.5–)2.3–2.4(–3.3) mm, linear to narrowly triangular; apex obtuse, reddish; corona filaments in 2 series; filaments of outer series 28 to 30, (2.7–)5.7–6.6(–17.7) mm, red with a white apex; filaments of inner series (0.9–)1.5–1.7(–2.7) mm; operculum 1.4–1.9 mm; androgynophore 14.7–29.1 mm, green; stamens with filaments (3.1–)4.1–4.8(–7.2) mm; anthers (3.5–)4.1–4.2(–4.7) × (1.3–)1.5–1.9 mm; ovary 2.3–7.3 × 1–3.2 mm, ellipsoid to obovoid, densely puberulous to villous; styles (2.6–)3.4–3.6(–4) × 0.2–0.3 mm; stigma (0.6–)0.8–1(–1.4) mm diam. Fruits (20–)32–35(–53) × (8–)12–13(–27) mm, ellipsoid or fusiform, slightly to sharply hexagonal, dark red; seeds (2.1–)2.5–2.9(–3.3) × (1.4–)1.7–1.9(–2.5) mm, transversely sulcate with 7 to 8 sulci, the ridges slightly rugulose.

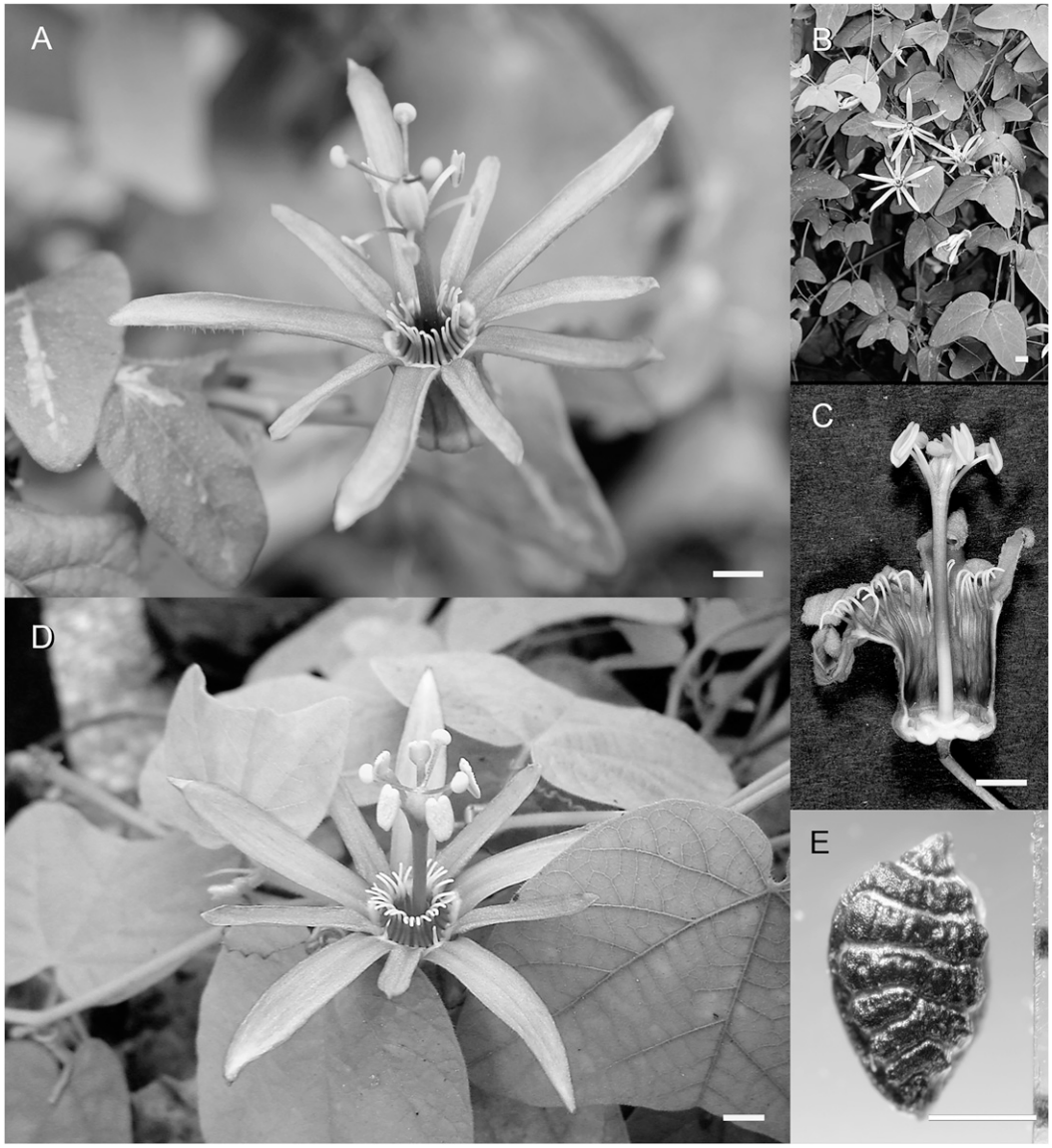

Figure 21. *Passiflora sanguinolenta* Mast. & Linden, all material originating from Ecuador and cultivated, except seed. —A. Flower. —B. Habit. —C. Flower in longitudinal section, wilted; note cuplike limen at base of androgynophore and a few vestigial inner corona filaments; cultivated at RSA (*S. Krosnick 389*). —D. Flower. —E. Seed; note rugulose ridges (*J. E. Madsen et al. 7830*). Scale bars: A, C, D = 0.5 cm; B = 1 cm; E = 1 mm. Photographers: A, Ronald Boender; B, Don Ellison; C, John MacDonald and Shawn Krosnick; D, Christian Feuillet; E, Tatiana Boza.

Phenology. Flowers of *Passiflora sanguinolenta* have been observed from September to February. Fruits have been documented in January, February, and September to November.

Distribution and habitat. *Passiflora sanguinolenta* is distributed in the mountains of southern Ecuador and northern Peru (Fig. 6). The taxon has been collected from 800 to 2800 m in elevation.

Discussion. *Passiflora sanguinolenta* was coined in Maxwell T. Masters's "New Plants" column in the *Gardener's Chronicle*, described in detail from a living specimen ("v. v."). Masters said, "We are indebted to M. Linden for specimens of this Passion-flower, collected by Mr. Wallis …" that is "a desirable acquisition for amateurs, and lovers of this singular genus," meaning amateur gardeners and horticulturists (Masters &

Linden, 1868: 1162). We expected to find a specimen at Kew collected by Linden or a cultivated specimen with Masters's handwriting from around this date but did not. Holm-Nielsen et al. (1988) saw a specimen at W of this species collected at Loja, Ecuador, by Gustav Wallis, unnumbered and without a date; the collector was possibly the same Wallis, but in any case, the collection would not be a type.

Masters actually cited two specimens in the protologue: the cultivated specimen of Linden and *Lobb 151* from "Peru" [Ecuador], which we have seen and is indeed referable to *Passiflora sanguinolenta*. One might argue that the two cited specimens are syntypes, but it is clear that the description was made only from the living material and the Lobb specimen should be considered a neotype. We are confident that the neotype chosen is representative of Masters's taxon.

The holotype of *Passiflora mastersiana* Harms was destroyed, so we have chosen one of the two isotypes housed at Kew as a lectotype. The one selected has well-preserved flowers and fruit available for future observations.

For comments on morphological similarity, see *Passiflora citrina*.

Selected specimens examined. ECUADOR. **El Oro:** Chaguarpamba–Balzas, 03°49′15″S, 079°48′15″W, *G. Harling et al. 20757* (AAU, GB). **Loja:** Las Juntas, 03°49′S, 079°16′W, 29 Sep. 1918, *J. N. Rose 23233* (GH, NY, US); Las Juntas–Pucála, 03°49′S, 079°16′W–03°51′S, 079°14′W, *F. C. Lehmann 4836* (B, F, GH, K, S, US); Pucala, N de Loja, *R. Espinosa E62* (US); Loja–San Lucas, 03°59′35″S, 079°12′15″W–03°45′00″S, 079°15′00″W, *A. S. Hitchcock 21470* (GH, NY, US); *A. S. Hitchcock 21494* (GH, NY, US); Km. 18.7, 3.7 km N of Solaman, 03°53′S, 079°13′W, *T. B. Croat & M. Menke 89968* (MO, US); Km. 19, 04°10′S, 079°10′W, *T. B. Croat 50839* (MO, QCA); Motupe, 6 km N of Loja, 03°56′32″S, 079°13′40″W, *E. Asplund 18048* (B, C, CAS, F, G, H, K, LL, NO, NY, PI, S, UC, UPS, US); 03°57′S, 079°14′W, *L. Albert de Escobar 1542* (CAS, LL, QCA, TEX); 03°57′S, 079°14′W, *L. K. Albert de Escobar 1540* (TEX); Motupe–Loja, 03°57′S, 079°14′W–04°00′S, 079°13′W, *L. K. Albert de Escobar 1539a* (LL, MO, TEX); Loja–Saraguro, Km. 2, 03°57′S, 079°13′W, *B. Øllgaard 57803* (AAU, MO, NY, U, UPS); Aguaedionda, N de Loja, *R. Espinosa 806* (US); Loja, 03°59′35″S, 079°12′15″W, *J. N. Rose 23900* (US); Catacocha, *R. Espinosa E-617* (US); Catacocha–Guano–Cariamanga, Km. 1.2–4.5, 04°03′50″S, 079°38′29″W, *P. M. Jørgensen et al. 1550* (MO, NY, QCA); Catacocha–Loja, Km. 10, 04°00′52″S, 079°36′19″W, *G. Harling et al. 15254* (AAU, GB); Km. 2–5 SE of Catacocha, 03°04′S, 079°36′W, *J. E. Madsen & O. A. Sanchez 7539* (AAU, MO); Cerro Villonaco, old rd. La Toma–Loja, 03°59′S, 079°16′W, *P. M. Jørgensen 65058* (AAU, QCA); Catacocha–Catamayo at Km. 10, approx. 8 km S along gravel rd., 04°03′09″S, 079°35′13″W, *J. E. Madsen et al. 7830* (AAU, MO); below Cangonamá toward Panamerican hwy. W of Catacocha, 03°59′S, 079°42′W, *H. Balslev 1342* (AAU, NY); Loja–Malacatos, Km. 20, 04°06′S, 079°12′W, *G. Harling & L. Andersson 18582* (AAU, GB, MO); Loja–Catamayo, Km. 22, 03°59′08″S, 079°18′06″W, *G. P. Lewis & B. B. Klitgaard 2400* (MO); Loja–Gonzanamá, via old rd. to La Toma, Km. 70.1, *J. L. Panero & B. L. Clark 2964* (MICH); San Pedro–Chinchas, 55 km O de Loja, *R. Espinosa E1314* (US); vic. of Chaguarbamba on Catamayo–Machala rd., ca. 21 km W of Las Chinchas, 03°57′S, 079°36′W, *S. Knapp & J. Mallet 9079* (MO); Catamayo, Km. 7 at Villonaco, 24 km along track to Cera & Chantaco & onward to La Toma, 03°59′57″S, 079°13′49″W, *G. P. Lewis & B. B. Klitgaard 3078* (K); Yangana–Cerro Toledo, *C. Ulloa 638* (GB, QCA); Vilcabamba–Yangana, *G. Harling & B. Ståhl 26305* (GB, QCA); 46 km S of Loja, Hacienda Anganuma, headwaters of Río Cachiyacu, 04°24′10″S, 079°09′01″W, *H. Jørgensen & J. P. Prieto 53* (NY, US); Vilcabamba–Cachiyacu, 04°15′S, 079°15′W–04°25′S, 079°08′W, *J. A. Steyermark 54397* (F, NY, US); Gonzanamá–Quilanga, Km. 8–9, 04°17′S, 079°27′W, *B. B. Klitgaard & G. P. Lewis 227* (AAU, MO, NY, QCA); Gonzanamá–Cariamanga, Km. 6, *G. Harling & B. Ståhl 26420* (GB); Cariamanga–Gonzanamá, 04°13′S, 079°33′W, *G. Harling & L. Andersson 18677* (AAU, GB, NY); N of Cariamanga, 04°18′04″S, 079°31′31″W, *G. Harling et al. 20634* (AAU, GB, US); Alamor–Cazaderos, just W of El Limo, *G. Harling & L. Andersson 22331* (GB, QCA); Alamor–Cazaderos, 6–7 km E of El Limo, 03°58′54″S, 080°03′58″W–03°59′27″S, 080°02′54″W, *G. Harling & L. Andersson 17911* (GB); Alamor–Puyango, Km. 12–15, 03°55′45″S, 080°01′07″W–03°57′53″S, 080°01′50″W, *G. Harling & L. Andersson 18000* (AAU, GB, QCA); Celica–Alamor at crossing with Río Alamor, *G. Harling & L. Andersson 22190* (GB, QCA). PERU. **Tumbes:** Zarumilla, Matapalo, El Caucho–Campo Verde, parcela de evaluación permanente "E," 03°50′46″S, 080°10′43″W, *C. Diaz et al. 7428* (MIN, MO); Matapalo, Naranjal–Campo Verde, 03°51′S, 080°10′W, *C. Díaz et al. 7462* (MO).

15. Passiflora tenella Killip, J. Wash. Acad. Sci. 20: 375. 1930. TYPE: Peru. Túmbez: SE of Hacienda La Choza, 100–200 m, 3 Mar. 1927, *A. Weberbauer 7704* (holotype, F [barcode] V0041738F!; isotypes, G!, G [bc] 00191102!, G [bc] 00191103 image!, K [bc] 000323360 image!, US photo at MO [bc] 3605735!). Figure 22.

Vines 10–90 cm, sparsely pilose to glabrescent throughout; stems subangular, striate. Stipules (1.1–)1.9–2.3(–3.5) × (0.1–)0.2–0.3(–0.5) mm, linear; petioles (9–)17–21(–30) mm; leaf laminas (1.3–)2.1–2.5(–3.2) × (3.2–)4.9–5.8(–7.6) cm, depressed obovate, cordate at the base, sparsely pilose abaxially with trichomes 0.5–1 mm, sparsely pilose adaxially with trichomes 0.6–1.2 mm, 3-lobed, the lateral lobes acute, the central lobe retuse or obtuse; angle between lateral veins (88°–)111°–119°(–134°). Peduncles (7–)15–18(–22) mm, solitary or rarely in pairs; floral stipe 0.4–0.9 mm, to 0.8–1.9 mm in fruit. Flowers (14.7–)15.1–15.9(–16.8) mm diam., greenish white; sepals (5.7–)7.6–8.3(–10.8) × (0.7–)1.3–1.7(–2.4) mm, narrowly linear or narrowly elliptic, sparsely pilose outside, apex acute, greenish white; petals (2.1–)2.9–3.3(–4) × 0.8–1(–1.1) mm, linear to narrowly triangular to narrowly ovate-elliptic, apex retuse to obtuse-rounded, greenish white; corona filaments in 2 series; filaments of outer series 20 to 26, (4.2–)6.1–7.1(–9.6) mm,

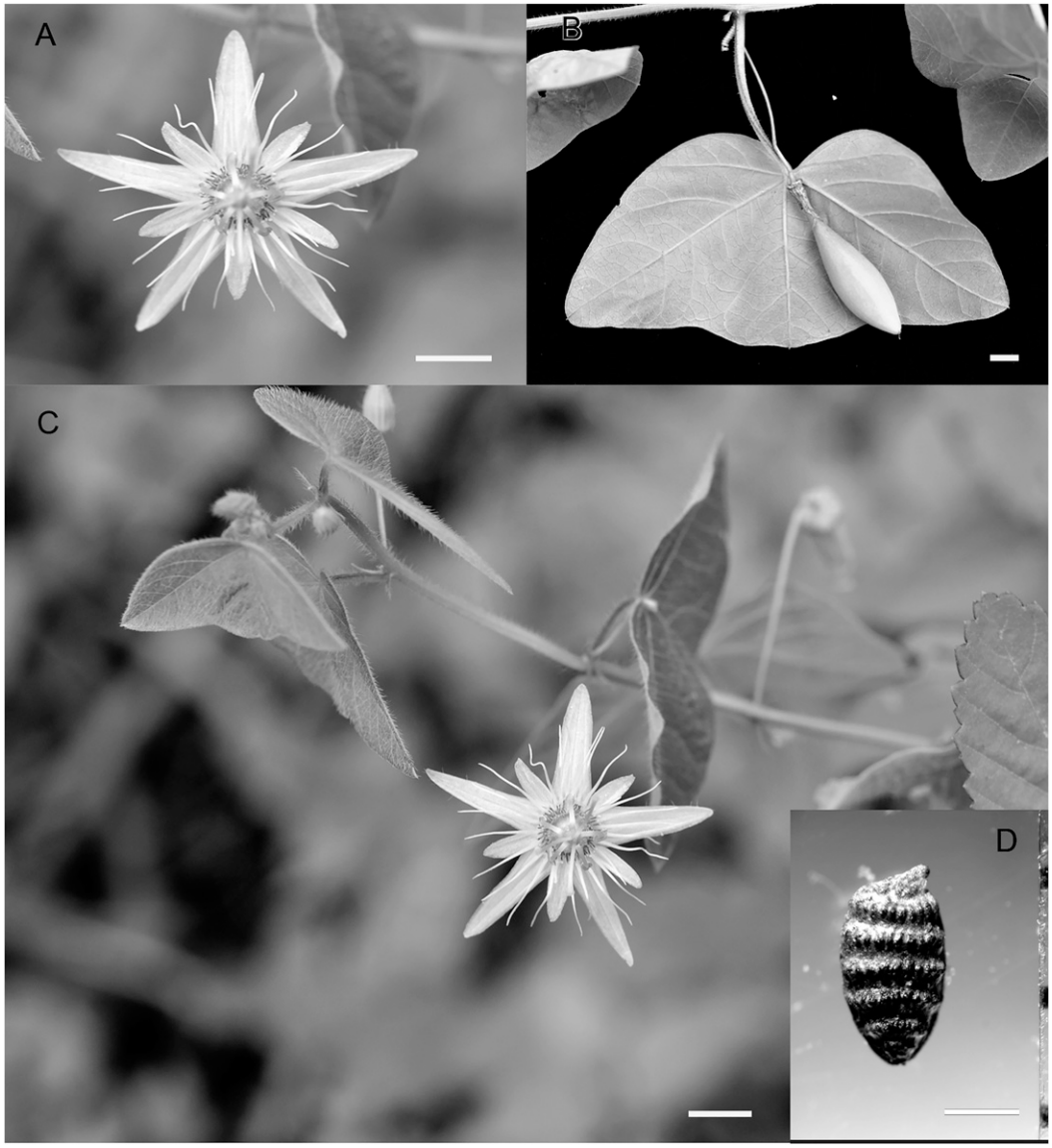

Figure 22. *Passiflora tenella* Killip, all from Ecuador, *P. M. Jørgensen 2455*. —A. Flower. —B. Leaf and immature fruit. —C. Habit, with shoot apex, leaves, buds, and flower. —D. Seed. Scale bars: A–C = 0.5 cm; D = 1 mm. Photographers: A–C, Peter M. Jørgensen; D, Tatiana Boza.

greenish white; filaments of inner series shorter than outer series, 0.9–1.1(–1.2) mm, violet-tinged; operculum (0.4–)0.7–0.9(–1.2) mm, slightly plicate; androgynophore 2.8–4.8 mm, green; stamens with filaments 2–2.3(–2.5) mm; anthers (1.1–)1.6–1.8(–2.1) × (0.6–)0.7–0.9(–1.1) mm; ovary 1.4–1.9 × 0.8–1.3 mm, narrowly ellipsoid, glabrous or rarely sparsely puberulous; styles (1.7–)2.5–3(–4.1) × 0.1–0.2 mm; stigma (0.2–)0.3–0.5(–0.6) mm diam. Fruits (17–)23–26(–32) × (5–)6–7(–11) mm, terete, not dehiscent, ellipsoid to fusiform, acuminate at the apex, 6-ribbed; seeds (2.3–)2.7–2.9 (–3.1) × 1.4–1.6(–1.8) mm, ovate, transversely sulcate with 4 to 5 sulci, the ridges strongly rugulose.

Phenology. Flowers and fruits of *Passiflora tenella* have been observed from January to April and in August and November.

Distribution and ecology. *Passiflora tenella* has been collected in dry coastal Peru and Ecuador (Fig. 7). The taxon has been collected in degraded primary dry forests from 0 to 450 m in elevation, primarily on forest edges and roadsides.

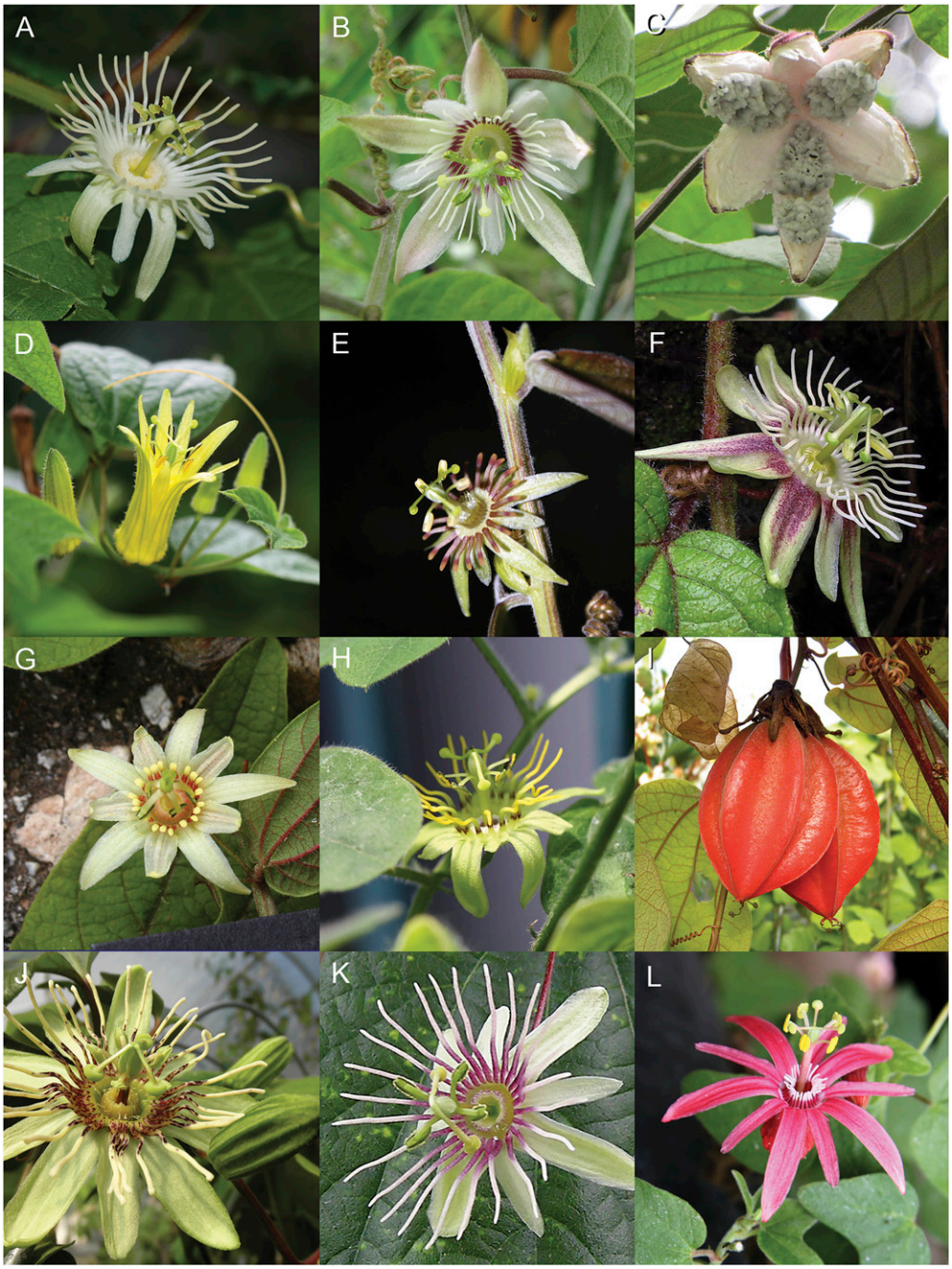

Figure 23. *Passiflora* L. sect. *Xerogona* (Raf.) Killip. —A. *Passiflora capsularis* L., flower showing unmarked corona, Dominican Republic. —B. *Passiflora cisnana* Harms, flower with coronal coloration only toward base, Peru (*T. E. Boza & P. O. Chambi 2044*). —C. *Passiflora cisnana* Harms, upward view into pendent dehisced fruit, Peru (*T. E. Boza et al. 2048*). —D. *Passiflora citrina* J. M. MacDougal, partially opened flower and buds, cultivated, origin Honduras. —E. *Passiflora cobanensis* Killip subsp. *brevipes* (Killip) T. Boza, flower and stipule, Quintana Roo, Mexico. —F. *Passiflora costaricensis* Killip, flower, Honduras. —G. *Passiflora goniosperma* Killip, flower near end of anthesis, Oaxaca, Mexico (*K. E. Porter-Utley 473*). —H. *Passiflora pusilla* J. M. MacDougal, flower, cultivated, origin Costa Rica. —I. *Passiflora rovirosae* Killip, mature but undehisced fruits, cultivated (*S. Krosnick 377*). —J. *Passiflora rovirosae*, flower and buds, cultivated (*S. Krosnick 377*). —K. *Passiflora rubra* L., flower with coronal coloration to near apex, cultivated, origin El Seibo, Dominican Republic. —L. *Passiflora sanguinolenta* Mast. & Linden, flower, cultivated, origin Ecuador. Photographers: A, Shawn Krosnick; B, C, Tatiana Boza; D, H, L, Ronald Boender; E, León Ibarra González; F, Shirley Sekarajasingham; G, Kristen Porter-Utley; I, J, Jorge Ochoa; K, Henk Wouters.

Discussion. *Passiflora tenella* is a poorly known species from dry coastal Ecuador and Peru that is apparently a diminutive annual; the plant reaches only 90 cm tall. The fruit does not appear to be a capsule, but rather terete and not dehiscent, and the seeds have transversely rugulose ridges that are somewhat different from other members of *Passiflora* sect. *Xerogona*, which have smooth ridges. However, the shape of the 3-lobed leaves and the absence of floral bracts and laminar nectaries suggest a placement within the section. Molecular studies based on four molecular markers, nuclear ribosomal ITS, ncpGS, chloroplast *trnL-F*, and *ndhF*, with a jackknife support of 70% for most clades along the backbone of the tree and for most *Decaloba* supersections (Krosnick et al., 2013), place *P. tenella* as basal to the rest of the section.

Selected specimens examined. ECUADOR. **El Oro:** Bosque Petrificado Puyango, 03°52′30″S, 080°05′01″W, *B. B. Klitgaard et al. 426* (AAU, MO, NY); *P. M. Jørgensen 2455* (MO, QCA, QCNE). **Guayas:** Capeira, Guayaquil–Daule, Km. 21, near entrance to el Matapalo, 02°00′S, 079°58′W, *C. H. Dodson & A. Gentry 12337* (MO); Nobol–Las Lomas del Sargentillo, 01°53′S, 080°05′W–01°55′S, 080°01′W, *G. Harling et al. 15680* (AAU, GB); near Soledad, 02°18′42″S, 079°17′04″W, *Haught 3052* (F, GH, K, S, UC, US); Isla Punà, vic. of Bellavista, 02°47′S, 080°13′W, *Madsen 63868* (AAU, MO, QCA); Guayaquil, 02°10′S, 079°54′W, *O. Haught 3523* (G, US). PERU. **Piura:** Huancabamba, Serran, 05°25′45″S, 079°46′25″W, *H. E. Stork 11374* (GH). **Tumbes:** Cherrelique–Cerros de Amotape, Km. 10, 04°05′S, 080°40′W, *A. Gentry & C. Diaz 58234* (MO); Tumbes, SE of Hacienda La Choza, 04°00′57″S, 080°39′54″W, *A. Weberbauer 7704* (B, F, G, K, MO, US); Contralmirante Villar, near La Huaca betw. Papayal & Cienago, 04°02′52″S, 080°44′49″W, *T. C. Plowman 5409* (GH).

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Appendix 1. *Passiflora* L. specimens measured for PCA analysis. The plant names used in this table are the names assigned to the specimens after this study.

Species	Senior Collector	Collection No.	Herbaria
P. capsularis	Bernardi, M.	18893	NY
P. capsularis	Cazalet, P. C. D.	5240	B, K, NY, UC
P. capsularis	Chase, M. A.	11060	GH, MICH, US
P. capsularis	Croat, T. B.	44486	MO
P. capsularis	Daviña, J.	206	CTES, G
P. capsularis	Eiten, G.	1844	GH, NY
P. capsularis	Fernández Casas, F. J.	5663	MA, MO
P. capsularis	Fiebrig, K. A. G.	6027	B, BM, E, G, GH, P, US
P. capsularis	Fonnegra, G. R.	5181	GH, HUA, MO, U
P. capsularis	Haber, W. A.	3932	MO
P. capsularis	Haber, W. A.	9536	MO
P. capsularis	Hamilton, C. W.	1260	MO
P. capsularis	Hassler, É.	7913	A, B, BM, G, GH, K, P, W
P. capsularis	Hassler, É.	11531	B, BM, C, E, G, GH, K, L, MO, NY, US, WIS
P. capsularis	Hatschbach, G. G.	36609	GH, HBG, MO
P. capsularis	Hatschbach, G. G.	45793	BR, G
P. capsularis	Haught, O. L.	6396	US
P. capsularis	Heyde, E. T.	6141	B, G, GH, US
P. capsularis	Howard, R. A.	163	GH
P. capsularis	Imaguire, N	1838	US
P. capsularis	Jardim, A.	1924	MO, NY, USZ
P. capsularis	Kalbreyer, W.	s.n.	HBG
P. capsularis	Knapp, S. D.	5500	MO
P. capsularis	Leonard, E. C.	9465	F, GH, US
P. capsularis	Lindman, C. A. M.	1141	GH, MO, S, UPS, US
P. capsularis	MacDougal, J. M.	685	DUKE
P. capsularis	Mamani, M. F.	1281	USZ
P. capsularis	Meyer, T.	11814	CTES
P. capsularis	Molina, R. A.	12920	EAP, F
P. capsularis	Moreno, P. P.	7907	MO
P. capsularis	Múlgura de Romero, M. E.	3091	MO, SI
P. capsularis	Múlgura de Romero, M. E.	1851	MO, SI
P. capsularis	Múlgura de Romero, M. E.	1909	MO, SI
P. capsularis	Pennell, F. W.	3424	GH, MO, NY, US
P. capsularis	Perdonnet, G.	264	G
P. capsularis	Rambo, B.	47127	B
P. capsularis	Reineck, E. M.	s.n.	HBG
P. capsularis	Reitz, P. R.	6116	US
P. capsularis	Ribas, O. S.	2227	C, G, HBG
P. capsularis	Rodríguez G., A.	5186	MO
P. capsularis	Rodríguez G., A.	5110	G
P. capsularis	Romanczuk, M. C.	486	BAB, SI
P. capsularis	Santa, J.	773	MO, NY
P. capsularis	Schinini, A.	19878	CTES
P. capsularis	Silva, J. M.	1944	C, G, HBG, MO
P. capsularis	Silva, J. M.	51	C, CAS
P. capsularis	Silverstone-Sopkin, P.	4044	MO
P. capsularis	Smith, H. H.	2780	NY
P. capsularis	Smith, L. B.	15012	GH
P. capsularis	Soria, N.	3491	FCQ, MO
P. capsularis	Uribe U., L.	2511	MA
P. capsularis	Woolston, A. L.	1206	C, GH, U
P. capsularis	Zardini, E. M.	47522	AS, MO, NY
P. capsularis	Zuloaga, F. O.	5095	MO, SI
P. capsularis	Zuloaga, F. O.	743	GH

Appendix 1. Continued.

Species	Senior Collector	Collection No.	Herbaria
P. cervii	Mexía, Y. E. J.	5402	CAS, G, GH, MO, NY, S, US
P. cervii	Oliveira, P. I.	691	HBG, NY, SP
P. cervii	Sehnem, A.	2430	CAS
P. cisnana	Bang, M.	2836	B, BM, CTES, G, GH, K, MICH, MIN, MO, NY, PH, S, US, W
P. cisnana	Beck, S. G	23428	LPB, MO
P. cisnana	Beck, S. G.	6367	LPB, M
P. cisnana	Beck, S. G.	22281	LPB, MO, NY
P. cisnana	Benítez de Rojas, C. E.	1173	F, MY, U
P. cisnana	Betancur, B. J.	4986	COL, MO
P. cisnana	Buchtien, O.	3852	GH, US
P. cisnana	Camp, W. H.	3014	G, GH, MO, NY
P. cisnana	Campos de la Cruz, J.	4813	MO
P. cisnana	Clarke, D.	858	US
P. cisnana	Díaz Santibáñez, C.	3197	MO
P. cisnana	Escobar, L. K. A. de	4824	F, HUA, LPB, MA, MO, QCA, TEX
P. cisnana	Harling, G. W.	22410	GB, QCA
P. cisnana	Harling, G. W.	22173	GB
P. cisnana	Jardim, A.	1555	MO, USZ
P. cisnana	Jiggins, C.	38	QCA
P. cisnana	Knapp, S. D.	2838	MO
P. cisnana	Knapp, S. D.	6323	BH
P. cisnana	Lasser, T.	1552	NY
P. cisnana	Lewis, G. P.	3499	E, K, MO
P. cisnana	Lewis, G. P.	3077	MO, QCA
P. cisnana	Madsen, J. E.	7412	AAU, MO, NY
P. cisnana	McDade, L. A.	1056	DUKE, MO
P. cisnana	McDade, L. A.	1027	DUKE
P. cisnana	Molina, A.	457	MO
P. cisnana	Rubio, D.	2364	MO
P. cisnana	Silverstone-Sopkin, P.	6184	MO
P. cisnana	Silverstone-Sopkin, P.	2573	MO
P. cisnana	Smith, J. F.	2046	QCA, WIS
P. cisnana	Stoffers, A. L.	186	B, MA, NY, U, US
P. cisnana	Ule, E. H. G.	6546	B, G, HBG, L
P. cisnana	Uribe, A. & Uribe, L.	3471	NY
P. cisnana	Valenzuela, L.	1356	CUZ, MO
P. cisnana	Weberbauer, A.	7653	F, G, US
P. cisnana	Weigend, M.	98/382	M, MO, USM
P. cisnana	Weigend, M.	98/185	M, MO
P. rubra	Abbott, W. L.	178	US
P. rubra	Acevedo-Rodríguez, P.	5642	NY
P. rubra	Alain, Brother	825	GH
P. rubra	Arbeláez, A. L.	621	MO, NY
P. rubra	Axelrod, F. S.	6178	MO, UPRRP
P. rubra	Axelrod, F. S.	2959	MO, NY, UPRRP
P. rubra	Axelrod, F. S.	5812	MO, NY, UPRRP
P. rubra	Britton, N. L.	1605	GH, K, NY, US
P. rubra	Brown, S.	29	NY, PH
P. rubra	Correll, D. S.	47009	MO, NY
P. rubra	Correll, D. S.	47860	F, MO, NY
P. rubra	Correll, D. S.	51385	DUKE, F, MO, NY
P. rubra	Day, E. H.	s.n.	K
P. rubra	Duss, A.	2231	B, C, F, NY, US
P. rubra	Ernst, W. R.	1987	GH, US
P. rubra	Fernández Casas, F. J.	10769	CAS, MO

Appendix 1. Continued.

Species	Senior Collector	Collection No.	Herbaria
P. rubra	Fontaine, D.	s.n.	G
P. rubra	Heller, A. A.	s.n. (11 Dec. 1902)	NY
P. rubra	Heller, A. A.	1218	F, K, NY, US
P. rubra	Hunnewell, F. W.	11381	GH
P. rubra	Leonard, E. C.	14120	MO, US
P. rubra	Leonard, E. C.	3668	NY, PH, US
P. rubra	Leonard, E. C.	3685	US
P. rubra	Maxon, W. R.	8800	GH, RSA, US
P. rubra	Mori, S. A.	26998	NY
P. rubra	Mori, S. A.	25953	NY
P. rubra	Nash, G. V.	746	NY
P. rubra	Nicolson, D. H.	1870	B, CAS, US
P. rubra	Proctor, G. R.	18885	A
P. rubra	Proctor, G. R.	6750	LL, NY
P. rubra	Rose, J. N.	3459	B, GH, NY, US
P. rubra	Smith, H. H.	607	B, E, GH, HBG, K, NY
P. rubra	Stevenson, J. A.	153	MIN, US
P. rubra	Webster, G. L.	10491	DUKE, GH
P. rubra	Webster, G. L.	8259	G
P. rubra	Wright, C.	201	BR, G, K, MO, NY, PH, S